Is Maungatautari restoring bird pollination and seed dispersal services?

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Bellbird feeding in a female *Fuchsia excorticata* tree, Maungatautari

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Abstract

The decline in range and density of many native New Zealand birds from mammalian predation has raised concerns over the functioning of ecosystem processes such as pollination and seed dispersal. At Maungatautari, almost all mammalian pests have been eradicated from within a pest-proof fence enclosing 3400 ha of native forest. I examined whether Maungatautari is restoring pollination and seed dispersal services to native plants, compared to a nearby non-treatment site, Pirongia Mountain.

Five-minute bird counts made at Maungatautari and Pirongia (in 2002 and 2005 prior to pest eradication from Maungatautari, and in 2008 and 2010 following eradication) indicated that 10 of the 12 individual bird species examined showed significant changes in abundance following pest control. Six species showed an increase in abundance, including bellbirds (*Anthornis melanura*), tui (*Prosthemadera novaeseelandiae*) and kereru (*Hemiphaga novaeseelandiae*). Counts of all native species combined increased at Maungatautari while counts of all exotic species showed no trend over count years.

In December 2010, 140 five-minute bird counts showed tui and bellbirds, key pollinators, to be more abundant at Maungatautari than Pirongia. Higher pollen loads on the stigmas of both female and hermaphrodite *Fuchsia excorticata* flowers at Maungatautari, compared to Pirongia, suggest that *F. excorticata* at Maungatautari received better pollination service. *Fuchsia excorticata* pollen loads collected from 67 sites around New Zealand indicate that female plants at sites with lower abundances of mammalian predators generally received better pollination service. Hermaphrodite *F. excorticata* plants had similar and high pollen scores in all regions, except for in the North Island.

Five-minute bird counts in December 2010 also showed that kereru and blackbirds (*Turdus merula*), key seed dispersers along with tui and bellbirds, were more abundant at Maungatautari than Pirongia. A second measure of bird abundance, maximum counts, showed flock sizes of tui, bellbirds and kereru were larger at Maungatautari, but only significantly so for tui and bellbirds. *Fuchsia excorticata* fruits were removed more rapidly from plants at Maungatautari than at Pirongia (a 6-fold difference). There was twice the density of tawa fruits (bird cleaned and fleshy) under trees at Maungatautari compared to Pirongia, perhaps from reduced mammalian fruit predation. There was no significant site effect on tawa dispersal service (percent of fruit consumed by birds), but a significant site x fruit density interaction, suggests birds at Maungatautari provided better dispersal service to large fruit crops. A similar number of miro fruit (bird cleaned and fleshy)

were caught in seed traps under miro trees, but a greater percentage of fruits were consumed by birds at Maungatautari (59%) compared to Pirongia (26%).

The results from this thesis indicate that increased densities of key native birds at Maungatautari are providing better pollination and dispersal services to the native plants examined. Projects which increase the density of key bird mutualists, such as tui, bellbirds and kereru, on the mainland, may have positive benefits for pollination and seed dispersal mutualisms.

Chapter 1

General Introduction

Birds provide a range of important ecosystem processes and services such as pollination, seed dispersal, scavenging, nutrient cycling, predation and ecosystem engineering (Sekercioglu 2006; Whelan et al. 2008; Wenny et al. 2011). However, birds are suffering from reductions in diversity and number worldwide, due to human actions including species introductions, exploitation, and habitat loss and fragmentation (Gaston et al. 2003; Sekercioglu et al. 2004; BirdLife International 2008; Butchart et al. 2010). Given the worldwide decline of birds, there is considerable concern about how well ecological processes and services reliant on birds are working (e.g., Cordeiro & Howe 2003; Sekercioglu et al. 2004; Peh et al. 2006; Chimera & Drake 2010; Kelly et al. 2010; Anderson et al. 2011). New Zealand is particularly vulnerable to the failure of bird-plant interactions, as the pre-human avifauna has been considerably altered, and a high proportion of trees are pollinated and dispersed by birds (Sekercioglu et al. 2004; Kelly et al. 2010; Anderson et al. 2011). In this thesis I examine whether a site on the New Zealand mainland with a high abundance of pollinating and dispersing birds has restored pollination and seed dispersal services. This introductory chapter gives an overview of the background to the topic, and there is more detail given on selected areas in the introductions to subsequent data chapters.

1.1 Reductions in the diversity and abundance of New Zealand birds

Similar to other island avifaunas which evolved without terrestrial mammalian predators, New Zealand's avifauna was particularly vulnerable to human colonisation and resulting environmental change (Steadman 1995; Blackburn et al. 2004; Innes et al. 2010). Following human arrival, almost a third of bird species breeding in the New Zealand region became locally or globally extinct (Holdaway et al. 2001; Worthy & Holdaway 2002), losses were particularly great for land bird species (Craig et al. 2000; Holdaway et al. 2001). Holdaway (1989) identified three phases of avian extinction and decline; the first two phases were associated with the arrival of Maori from Polynesia (from approximately 1280 AD (Wilmshurst et al. 2008)), and last and continuing phase was associated with European arrival (from around 1780 AD). Extinctions resulted from hunting by humans, predation and competition from introduced mammals, and habitat loss and fragmentation (Holdaway 1989). Holdaway concluded that introduced predators, including humans, were the principal cause of extinction (Holdaway 1999; Worthy & Holdaway 2002).

The effects of mammalian predation upon New Zealand's remaining birds are ongoing. Several endemic forest bird species have been lost from the mainland, despite large areas of native forest habitat remaining (Elliott et al. 2010). For example, kakapo (*Strigops habroptilus*), only remain on predator-free offshore islands and are extremely vulnerable to extinction (Powlesland et al. 2006). Predatory mammals are considered to be the main cause of continuing population declines within large native forest tracts (reviewed by Innes et al. 2010). Even relatively common endemic species which appear to have stable and secure populations are reduced in abundance by mammal predators (Innes et al. 2010), although recent work suggests that even some of these species may be declining undetected in some areas (Elliott et al. 2010). The current forest bird avifauna is thus characterised by populations which are often reduced in range, are declining, and/or are at low densities (Craig et al. 2000; Innes et al. 2010).

Sekercioglu et al. (2004) defined bird species that are endangered, critically endangered, or extinct in the wild as "functionally extinct", and as "functionally deficient" those species that have recently experienced substantial reductions in abundance, and/or extent or occupancy of geographic range. The large reductions in range and density of many New Zealand bird species may be rendering them functionally extinct, where they are no longer contributing to ecosystems processes, or functionally deficient, where the amount they now contribute is negligible.

1.1.1 Mammalian predator control and forest birds

Mammalian predator control is critical for the protection of many threatened and endangered endemic species on the New Zealand mainland (the large and highly modified North and South Islands) (McLennan et al. 1996; Innes et al. 1999; Moorhouse et al. 2003; Innes et al. 2010). Control of mammalian predators also increases the abundance of some common endemic species, such as bellbirds (korimako, *Anthornis melanura*) and tui (*Prosthemadera novaezelandiae*) (Innes et al. 2004; Kelly et al. 2005; O'Donnell & Hoare 2012). In recognition of the detrimental impacts of mammalian predation on native bird populations, and the benefits gained from controlling predators, mammalian pest control is prevalent in New Zealand. Pest management is currently conducted at a range of intensities and scales (O'Donnell et al. 1996; Dilks et al. 2003; Gillies et al. 2003; Innes et al. 2012). One recently developed intensive form of pest management is fenced sanctuaries. These are sites which have been encircled by a mammal pest-proof fence, and are valuable in allowing eradication of all mammalian pests from areas on the mainland (Speedy et al. 2007). Fenced sanctuaries have enabled several forest bird species highly vulnerable to mammalian predation to be reintroduced to the mainland, such as hihi (stitchbirds, *Notiomystis cincta*), North Island saddlebacks (*Philesturnus carunculatus rufusater*) and little spotted kiwi (*Apteryx owenii*) (Innes et al. 2010).

1.2 Bird-plant mutualisms: pollination

Pollination is necessary for sexual reproduction in plants (Proctor et al. 1996). Approximately 88% of extant terrestrial flowering plant species are animal-pollinated (Ollerton et al. 2011). While most animal-pollination is by insects (Proctor et al. 1996), over 920 bird species are involved in pollination (Whelan et al. 2008). Bird pollination is most common in the tropics, New Zealand and Australia (Sekercioglu 2006). Birds may be advantageous pollinators over insects, by: being more reliable in cold weather conditions when invertebrates are inactive; having greater surface areas for the attachment of pollen; visiting many flowers frequently and travelling further between feeding bouts, hence increasing gene flow between plants (Ford et al. 1979; Ford 1985; Sekercioglu 2006; Whelan et al. 2009). They may be particularly valuable pollinators of plants which are self-incompatible and have patchy distributions (Sekercioglu 2006). Reductions or loss of pollinators can cause pollen-limitation, where plant reproductive success is reduced by inadequate quantity or quality of pollen (Ashman et al. 2004). Pollen-limitation can have direct impacts on population viability and demographics (Aizen et al. 2002; Wilcock & Neiland 2002; Anderson et al. 2011).

1.2.1 Pollination in New Zealand

The New Zealand flora has a high reliance on biotic pollen vectors, with approximately 71% of native seed plant genera pollinated by animals (Webb et al. 1999). New Zealand has a low diversity of indigenous pollinating fauna, and specialised pollinators are rare compared to elsewhere (Heine 1938; Godley 1979; Primark 1983; Lloyd 1985; Webb & Kelly 1993; Newstrom & Robertson 2005). Pollinators in New Zealand are insects, birds, bats and lizards (Newstrom & Robertson 2005; Pattemore & Wilcove 2012). Reliance on pollinators is elevated because of the sexual systems present (Newstrom & Robertson 2005); sexual dimorphism, particularly dioecy (male and female flowers occur on separate plants), is unusually common in the New Zealand flora compared to continental areas (Lloyd 1985; Webb & Kelly 1993; Webb et al. 1999). New Zealand flowers are predominantly small, structurally simple and pale in colour, and flowers are often amassed into large inflorescences; characteristics of flowers considered to be generalised and entomophilous (apparently insect-pollinated, see Faegri & van der Pijl 1979) (Heine 1938; Godley 1979; Lloyd 1985; Castro & Robertson 1997; Newstrom & Robertson 2005). Plants with ornithophilous (apparently bird pollinated, see Faegri & van der Pijl 1979) flower structures are uncommon in the flora, with only 29 species (Kelly et al. 2010).

1.2.2 Bird pollination in New Zealand

Bird pollination was initially considered unimportant in New Zealand (Godley 1979; Lloyd 1985; Clout & Hay 1989) due to the low diversity of potential endemic bird pollinators and the lack of plants with apparent adaptations for bird pollination (Ford et al. 1979; Godley 1979; Lloyd 1985). Instead, it was thought that insects, which visit many ornithophilous flowers, could replace birds in their pollination (Godley 1979; Clout & Hay 1989). Although Godley (1979) and Clout and Hay (1989) did caution that to understand the importance of birds as pollinators it was important to examine the end result of pollination (i.e. seed set).

The view that bird pollination was unimportant in the New Zealand flora continued until the 1990's, when a series of studies began to accumulate evidence to the contrary (Ladley & Kelly 1995; Anderson 1997; Castro & Robertson 1997; McNutt 1998; Heenan & deLange 1999). It was revealed that birds regularly visit flowers considered to have entomophilous syndromes (Anderson 1997), these flowers are profitable to forage upon (Castro & Robertson 1997), and bird visitation improves seed set (Anderson 2003). Birds are important pollinators of winter flowering plants, such as five-finger (*Psuedopanax arboreus*), when indigenous bees and other pollinating insects are less active (Anderson 1997, 2003; Newstrom & Robertson 2005). Pollen-limitation has been demonstrated in a number of ornithophilous plants (Robertson et al. 1999; Montgomery et al. 2001; Newstrom & Robertson 2005; Anderson et al. 2006; Kelly et al. 2007; Merrett et al. 2007; Robertson et al. 2008; Anderson et al. 2011), indicating that bird visitation is often necessary for high seed set, and pollination failure can have demographic consequences (Anderson et al. 2011). Where pollination of ornithophilous species has been examined when accessible only to insects, pollination has been reduced (Anderson 2003; Robertson et al. 2005). Reductions in pollination suggests insects are inefficient pollinators of ornithophilous flowers due to a size mismatch, as they either fail to contact the stigma or rob nectar through the corolla (Kelly et al. 2010).

Currently, birds are believed to visit the flowers of 85 plant species and bird pollination is thought to be important for reproduction in 48 of these species (Kelly et al. 2010). Godley (1979) considered 10 bird species (eight native and two exotic) to be visitors of native flowers and Kelly et al. (2006) added a further seven species (four native and three exotic). The latest compilation by Kelly et al. (2010) brought the total to 17 species (12 native and five exotic). No native bird pollinators are believed to have become extinct following human settlement (Atkinson & Millener 1991), but several species are "functionally extinct" on the New Zealand mainland. For example, hihi, kaka (*Nestor meridionalis*) and kokako (*Callaeas cinerea*) were probably important flower visitors before becoming severely reduced in range and density, as they have brush tongues adapted for nectar consumption (Kelly et al. 2010). Additionally, hihi made 15% of flowers visits on Tiritiri

Matangi and Little Barrier Islands where they still occur (Kelly et al. 2006). At present most flower visitation (89%) is made by tui, bellbirds and silvereyes (*Zosterops lateralis*) (Kelly et al. 2006). All three species also have brush tongues (McCann 1964; Heather & Robertson 1996). Only the self-introduced silvereye remains widespread and abundant, as bellbirds and tui have decreased in abundance and disappeared from some areas (Kelly et al. 2006).

1.3 Bird-plant mutualisms: dispersal

Dispersal of seeds is a critical process in the life history of plants, affecting plant community structure and function (Howe & Smallwood 1982; Nathan & Muller-Landau 2000; Herrera 2002; Schupp et al. 2010). Plants rely on a variety of abiotic (wind, water and gravity) and biotic vectors to transport their seeds (Howe & Westley 1986). Animals disperse seeds either by epizoochory, where seeds are externally attached to animals, or by endozoochory, the dispersal method of interest in this thesis, where seeds are consumed by an animal and are later either defecated or regurgitated in a viable state (van der Pijl 1982; Sorenson 1986). In most plant communities birds and mammals are the main animal seed dispersers (van der Pijl 1982; Herrera 2002). Birds are ideal endozoochorus seed dispersers as they are widespread, highly mobile, can travel long distances and typically swallow fruits and seeds intact (Whelan et al. 2008).

1.3.1 Dispersal of fruits in New Zealand

Approximately 12–14% of indigenous New Zealand plant species produce fleshy fruit, indicative of adaptation for seed dispersal by frugivores (Lord et al. 2002; Thorsen et al. 2009). This proportion is higher amongst tree species, with 59% of trees having fleshy fruit (Kelly et al. 2010). Most New Zealand fruits are small in size, with an overall mean diameter of 6.4 mm (Lord et al. 2002), although the largest species, taraire (*Beilschmiedia tarairi*), has fruits which average about 20 mm in diameter (Kelly et al. 2010). New Zealand has a relatively depauperate disperser fauna (Webb & Kelly 1993). The main frugivores in New Zealand are birds (Clout & Hay 1989; Lee et al. 1991) and reptiles (Whitaker 1987; Lord et al. 2002; Wotton 2002). Bats (Daniel 1976) and possibly weta (Orthoptera, Duthie et al. 2006, but see Wyman et al. 2011), may also do some dispersal.

New Zealand native fruits tend to become more elliptical with increasing size, possibly due to selective pressures on fruit size resulting from the relatively small size of most volant (flighted) birds (Lord et al. 2002). Increased elongation with greater fruit size maintains "swallowability" while allowing fruit mass to increase (Lord et al. 2002), this may allow mid-sized birds, such as tui,

kokako and saddlebacks, to eat the fruits of mid-sized plant species and also the smaller fruits of the largest-fruited species (Kelly et al. 2010). Fruits are most often reddish in colour (67%, Lee et al. 1991), although orange, black, purple, blue or white fruit also occur (Poole & Adams 1963; Lee et al. 1991; Williams & Karl 1996). New Zealand has an unusually high proportion of white and blue fruits, perhaps indicating lizards are important dispersers of some species (Lord et al. 2002).

1.3.2 Bird dispersal in New Zealand

The seed dispersing avifauna has been more drastically altered by human arrival in New Zealand than the pollinating avifauna. Four frugivorous bird species (piopio *Turnagra capensis*, huia *Heteralocha acutirostris* and two moa species that had small gizzard stones (*Euryapteryx* spp.)), thought to have been important dispersers are now extinct (Atkinson & Millener 1991; Anderson et al. 2006). While the severely restricted range of others (hihi, saddlebacks *Philesturnus carunculatus* and North Island kokako *Callaeas cinerea wilsoni*), has rendered them functionally extinct over most of the mainland (Anderson et al. 2006; Miskelly et al. 2008). Kelly et al. (2006) list 22 bird species (15 native and seven introduced) as current fruit visitors, however, 84% of visits to fruit were made by just four bird species; kereru (*Hemiphaga novaeseelandiae*), tui, bellbirds and silvereyes (Kelly et al. 2006). Kereru, like tui and bellbirds, are currently reduced in density on the New Zealand mainland (Kelly et al. 2006).

Unlike bird pollination, bird dispersal in New Zealand has long been considered important. There has been frequent concern in the literature about dispersal failure (especially for large fruits) related to reduced diversity and densities of frugivorous birds (especially of kereru) in New Zealand (e.g., McEwen 1978; Clout & Hay 1989; Lee et al. 1991; Clout & Tilley 1992; Webb & Kelly 1993; Craig et al. 2000; Norton 2009). Kereru were said to be the only extant common forest bird capable of dispersing large-seeded fruits (>14 mm diameter), and the main dispersers of medium sized fruits (10–14 mm diameter) (McEwen 1978; Clout & Hay 1989). Additionally, frugivore gut passage was considered crucial for the germination of many species (e.g., Burrows 1995, 1996a, 1996b; 1999).

However, dispersal may be less at risk than previously thought (Anderson et al. 2006; Kelly et al. 2010). Recently, it has been shown that other birds with smaller gapes, such as tui and bellbirds, can swallow some of the smaller individual fruits of nearly all the large-fruited species, leaving taraire as the only plant species that is "entirely dependent" on kereru for dispersal (Kelly et al. 2010). The requirement of fruit flesh removal by frugivores for germination found by Burrows (1995, 1996a, 1996b; 1999), appears to be an artefact of the experimental methods used. Burrows examined germination of hand-cleaned and fleshy fruits in petri dishes and found that the fleshy

fruits had very low germination rates compared to clean seeds (Burrows 1995, 1996a, 1996b; 1999; reviewed by Kelly et al. 2004). It is thought that petri dishes prevent germination inhibitors in the flesh from leaching away (Robertson et al. 2006; Kelly et al. 2010). More relevant tests, of germination of clean and fleshy fruits on soil, indicate that all 18 of the fleshy-fruited species tested were able to germinate in their flesh (Robertson et al. 2006; Kelly et al. 2010), which is important because it indicates that fruits of these species that are not ingested by frugivores can germinate. The level of dispersal service by birds to 10 fleshy-fruited species has been examined so far, of which, seven were interpreted by Kelly et al. (2010) as receiving good dispersal service, two slow and one poor. The seven species considered to have good dispersal (tawa *Beilschmiedia tawa*, miro *Prumnopitys ferruginea*, and five species of mistletoe: *Peraxilla colensoi*, *Peraxilla tetrapetala*, *Alepis flavida*, *Ileostylus micranthus* and *Tupeia antarctica*) were all examined on the New Zealand mainland where bird densities are presently reduced. However, the two species with slow dispersal (*Fuchsia excorticata* and nikau *Rhopalostylis sapida*) and one with poor dispersal (karo *Pittosporum crassifolium*) were contrasts between the mainland and island bird sanctuaries with high density and diversity of dispersing bird species (Kelly et al. 2010). These mainland/island contrasts suggest that the decreased abundance and diversity of birds on the mainland may be having negative effects upon seed dispersal.

1.4 Risk of mutualism failure causing plant population decline or extinction

The risk of plant extinction resulting from mutualist failure depends on three criteria (Bond 1994). Firstly, the likelihood of mutualists providing inadequate pollination or dispersal services (Bond 1994). This is influenced by the level of specialisation of the mutualism, how many animal species are involved and whether species are substitutable (Bond 1994; Johnson & Steiner 2000; Kelly et al. 2004). Plants pollinated or dispersed by a single species or a few ecologically similar species may be particularly vulnerable (Bond 1994; Christian 2001; Aizen et al. 2002; Riera et al. 2002). For bird-dispersed species, increasing vulnerability is associated with increasing fruit or seed size (Bond 1994; Terborgh et al. 2008). The level of mutualist service can be quantified by the rate of fruit or flower visitation (Kelly et al. 2004). The number of visits to seeds and the number of seeds removed by frugivores provides a measure of dispersal quantity (Schupp 1993; Schupp et al. 2010). How dispersers treat seeds in their mouth and gut, and where seeds are deposited is also important, and this is termed ‘dispersal quality’ (Schupp 1993; Schupp et al. 2010).

The second criterion is how dependent reproduction is on the mutualism (Bond 1994). For pollination this largely depends on the breeding system (sex system plus mating system) of the

plant species. Dioecious and self-incompatible species are highly dependent on pollination, while self-compatible and autogamous hermaphroditic species are less dependent (Bond 1994; Wilcock & Neiland 2002). Many animal-pollinated plant species have mixed mating systems (both selfing and outcrossing), which may provide some reproductive assurance by allowing individuals to self-pollinate when pollinators are scarce or unpredictable (Barrett 2002; Ollerton et al. 2011).

The reproductive dependence on dispersal mutualisms depends on how strongly dispersal affects germination or recruitment and is likely to function on a continuum, with high dependence for some species and low for others (Bond 1994; Kelly et al. 2004). Gut treatment by frugivores may be necessary to cue germination (Bond 1994), and this concept has attracted a large amount of experimentation, but there is very little evidence in support of it (Rick & Bowman 1961; Traveset 1998; Samuels & Levey 2005; Robertson et al. 2006). Rather, under field conditions dispersal primarily functions to increase germination speed (Traveset 1998), which may or may not be beneficial (Kelly et al. 2004; Robertson et al. 2006). Perhaps more importantly, dispersal appears to be important in facilitating the escape from density-dependent natural enemies acting near the parent, the so-called Janzen-Connell effect (Janzen 1970; Connell 1971; Howe & Smallwood 1982; Packer & Clay 2000; Wotton & Kelly 2011). The reproductive dependence on pollination can by quantified by examining the sensitivity of reproduction to reduced pollinator visitation (i.e. testing for pollen-limitation) (Kelly et al. 2004). However, it is much harder to examine for dispersal as it depends on the relative fate of dispersed and undispersed seeds (Kelly et al. 2004). Examination of germination and density-dependent effects acting upon undispersed and dispersed seeds may provide some indication of the necessity of dispersal for germination and recruitment.

The third criterion is the demographic dependence of a population on seeds, namely how much continued seed production or dispersal is necessary to maintain plant population density (Bond 1994; Kelly et al. 2004). Bond (1994) considered that dependence on seeds is low when species are long-lived, produce many small seeds, are capable of clonal or vegetative propagation, and are able to resprout following disturbance, and dependence on seeds is high in species with short lifespans, low seed output and no seed bank. Plant populations which are microsite-limited may also be little affected by reduced seed production, as reductions in seed output simply reduce density-dependent thinning of seedlings with no effect on the density of adults (Bond 1994; Ashman et al. 2004). Seed dependence is tested using seed addition experiments to determine if populations are seed-limited (Turnbull et al. 2000; Kelly et al. 2004). Seed limitation for dispersal mutualisms is complicated by interactions between dispersal and distance, thus examination of the benefits of dispersal to a species' population size may give an indication of its importance (Kelly et al. 2004).

Reductions in pollination or dispersal services may have little impact on plant populations if they have compensatory mechanisms. Plants may compensate by being high risk in one of these areas and low risk in the other areas (Bond 1994, but see Aizen et al. 2002). For example, a plant reliant on a few specialised pollinators may self-pollinate when pollinators are not available or may be long-lived with large seed banks.

1.5 Effects of reduced mutualist diversity and/or density on mutualism functioning

Worldwide, there is evidence of reduced diversity and/or abundance of animal mutualists causing declines in, and occasionally failure of, the mutualism service provided to plants. For instance, reductions in frugivore abundance can decrease the dispersal service received by plants (Riera et al. 2002; Cordiero & Howe 2003; Terborgh et al. 2008; Chimera & Drake 2010) and may result in plant population declines (Christian 2001; Traveset & Riera 2005; Sharam et al. 2009; Traveset et al. 2012) and changes in species composition (Terborgh et al. 2008; McConkey et al. 2012). Similarly, reductions in the number and diversity of pollinators may decrease flower visitation rates and seed production (Steiner & Whitehead 1996; Paton 2000; Rathcke 2000; Mortensen et al. 2008), occasionally with demographic consequences (Anderson et al. 2011). Island ecosystems appear especially vulnerable to mutualism failure, particularly failures caused by biological invasions (Traveset & Richardson 2006). Island pollinating and dispersing animal species have frequently been eliminated or severely reduced by the introduction of predators to which native fauna lack appropriate defensive adaptations (Cox & Elmqvist 2000; Hansen et al. 2002; Traveset & Riera 2005; Mortensen et al. 2008).

In New Zealand, it appears that the reduction in native birds due to mammalian predation is having negative consequences on the pollination and dispersal services received by native plants. On the mainland where the abundance and diversity of native pollinators is low, many ornithophilous species are pollen-limited (Kelly et al. 2010; Anderson et al. 2011) and some are seed-limited (Bell 2010; Anderson et al. 2011). While dispersal services generally appear to be working adequately (Kelly et al. 2010), slower or poor fruit removal rates on the mainland compared to island bird sanctuaries, which have a high diversity and density of pollinating birds, indicates that dispersal services are also reduced on the mainland (McNutt 1998; Anderson et al. 2006; Robertson et al. 2008). Reductions in dispersal on the mainland may be having negative consequences on regeneration (Wotton & Kelly 2011). These demonstrations of pollination failure and reduced dispersal on the mainland are all occurring where plants are accessible to all introduced animal species. Therefore, while species such as honeybees (*Apis mellifera*), starlings (*Sturnus vulgaris*),

ship rats (*Rattus rattus*) and brushtail possums (*Trichosurus vulpecula*) may be doing some pollination and/or dispersal (Lord 1991; Williams & Karl 1996; Dungan et al. 2002; Kelly et al 2006; Pattemore & Wilcove 2012), it is clearly often insufficient to prevent pollination failure or reduced dispersal.

1.6 Restoration of mutualisms

Given the evidence that some mutualisms are failing, and their importance in maintaining and generating biodiversity, is it possible to restore them? There has been some interest in restoring animal-plant mutualisms in the literature (e.g., Traveset & Richardson 2006; Dixon 2009; Kaiser-Bunbury et al. 2010; Menz et al. 2011; Brodie & Aslan 2012). Restoration of insect-pollination mutualisms is predominant in agricultural settings due to the economic benefits gained from their reinstatement (Dixon 2009; Menz et al. 2011). Enhancement of seed dispersal by birds has been used to restore degraded or deforested lands (Robinson & Handel 1993, 2000; Zanini & Ganade 2005; Whelan et al. 2008) and the restoration of insect-pollination systems have been used as measures of ecological restoration success (Forup & Memmott 2005; Forup et al. 2008). However, there is little evidence of direct attempts to restore mutualisms in natural ecosystems (Dixon 2009; Menz et al. 2011). Baskett et al. (2011) improved the pollination service received by a native threatened plant by experimentally removing two invasive plant species which were competing for pollinator visitation with the threatened plant and increasing the transfer of interspecific pollen.

Given that the failure of bird-plant mutualisms on the New Zealand mainland appears to be related to reduced diversity and abundance of native bird mutualists, it may be possible to restore bird services by increasing native bird abundance. Kelly et al. (2005) attempted to restore a pollination mutualism by increasing the abundance of bellbirds, and although bellbird numbers successfully increased, there was no benefit to the pollination levels of *Peraxilla tetrapetala*. The current conservation approach in New Zealand, where multiple mammalian pest species are controlled over relatively large areas on the mainland, which successfully increases numbers of some native bird species (Innes et al. 2010), may be having indirect and as yet unmeasured benefits on bird-plant mutualisms such as pollination and seed dispersal (Anderson et al. 2006; McAlpine & Wotton 2009).

1.7 Thesis objectives

The overall objective of this thesis is to examine whether Maungatautari, a fenced sanctuary on the New Zealand mainland, is indirectly restoring the pollination and dispersal services to native plants through the increased abundance of key bird mutualists. To achieve this, Maungatautari, a site from which almost all mammalian pests have been eradicated, is compared to a nearby non-treatment site with a much lower level of mammalian pest control, Pirongia Mountain. The pest control at Maungatautari has been undertaken by the Maungatautari Ecological Island Trust, who are also monitoring pest abundance. Reduced mammalian pest densities may be affecting bird densities, which consequently may be affecting bird services; I tested several of the possible subsequent changes following pest control, from increased bird densities to better pollination and dispersal, as shown in Figure 1.1.

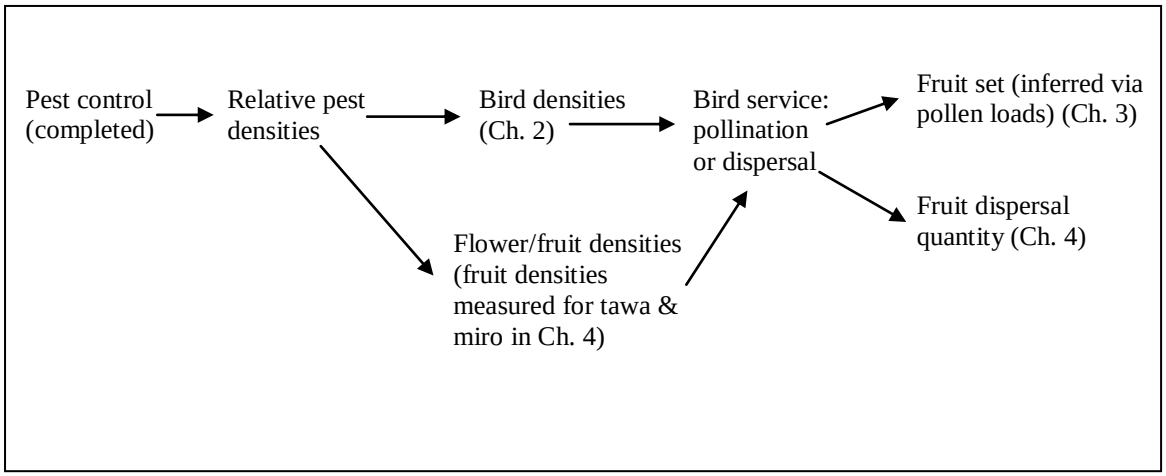

Figure 1.1: Outline of thesis chapters, separated by what may be happening at Maungatautari in response to pest control.

Specifically, the three following questions will be addressed:

1. Has the near-eradication of mammalian pests from Maungatautari increased the abundance of native bird species? (Chapter 2)

2. Has Maungatautari restored bird pollination of *Fuchsia excorticata*, a widespread native plant which is frequently pollen-limited at mainland sites? (Chapter 3)

3. Has Maungatautari restored bird dispersal services to three native plants (*F. excorticata*, tawa *Beilschmiedia tawa* and miro *Prumnopitys ferruginea*)? (Chapter 4)

In the final chapter (Chapter 5), I synthesise the findings of each chapter and discuss the overall implications of the results.

Chapters 3 and 4 are written as stand-alone papers, intended for later publication so there is some repetition in the introductions and methods. Chapter 2 is not intended for publication in this form, as this chapter uses five-minute bird counts provided by Landcare Research which they plan to later publish, but is written in a similar format to Chapters 3 and 4 to maintain consistency.

Chapter 2

The Effect of Mammalian Pest Removal from Maungatautari on the Abundance of Birds

2.1 Introduction

Human arrival in New Zealand approximately 700 years ago (Worthy & Holdaway 2002; Wilmshurst et al. 2008), drastically altered the diverse avifauna (Holdaway 1989; Atkinson & Millener 1991). Of the 245 bird species breeding in the New Zealand region at the time of human arrival, 31% are now locally or globally extinct (Holdaway et al. 2001). Losses were even greater on the main islands where human impacts were highest, with 51% and 47% of species lost from North and South Islands, respectively (Holdaway et al. 2001). Most of these losses can be attributed to the effects of introduced mammalian predators, including humans (Holdaway 1999; Duncan et al. 2002). The New Zealand avifauna evolved with only avian predators (Holdaway 1989) and consequently had characteristics which increased their vulnerability to mammalian predation, for example, low fecundity, flightlessness, tameness, naivety, ground feeding, and ground and cavity nesting (Moors 1983; Holdaway 1989; Beggs & Wilson 1991; Lovegrove 1996; McLennan et al. 1996; O'Donnell 1996; Worthy & Holdaway 2002; Duncan & Blackburn 2004).

The effects of introduced predators, particularly mustelids (*Mustela* spp.), rats (*Rattus* spp.), cats (*Felis catus*) and brushtail possums (*Trichosurus vulpecula*), on native birds are on-going (Innes & Hay 1991; Brown et al. 1993; Wilson et al. 1998; Innes et al. 2010). The present day avifauna is characterised by many small and declining populations, with 55% of extant New Zealand forest birds currently classified as endangered, threatened or declining (Hitchmough et al. 2007; Innes et al. 2010). In remaining large native forest areas, mammalian predation is considered the main cause of decline and limitation on population size of forest birds (Innes et al. 2010). However, research has shown that predator control can successfully protect some bird species, prevent local extinction and lead to recovery (e.g. kaka *Nestor meridionalis*, Moorhouse et al. 2003; North Island kokako *Callaeas cinerea wilsoni*, Innes et al. 1999; mohua *Mohoua ochrocephala*, O'Donnell et al. 1996; kiwi *Apteryx* spp., McLennan et al. 1996).

There are several lines of evidence that predatory mammals may be an important factor limiting even common species of native birds. Firstly, predator control improves nesting success (e.g. kereru *Hemiphaga novaeseelandiae*, Clout et al. 1995; Innes et al. 2004; bellbirds *Anthornis melanura*, Kelly et al. 2005; bellbirds and grey warblers *Gerygone igata*, Starling-Windhof et al.

2011), and increases the abundance of particular species (e.g. kereru, Gillies et al. 2003; bellbirds, Kelly et al. 2005; tui *Prosthemadera novaeseelandiae*, O'Donnell & Hoare 2012). Secondly, native birds reach much higher densities on offshore islands without all or most mammalian predators compared to the New Zealand mainland (Diamond & Veitch 1981). For example, Bartle and Sagar (1987) found bellbirds on the Poor Knights Islands were 54 times more abundant than at South Island sites. However, the effects of predator control on bird populations are complicated. Rats and possums are omnivorous, so controlling predators may also increase the food supply available to birds (Innes et al. 2010). Additionally islands are ecologically different from the mainland and have different limiting factors (Innes et al. 2010).

In contrast to native species, many bird species introduced to New Zealand have become very common, sometimes even more abundant than in their native range, despite being subject to the same suite of predators as native birds. New Zealand has about 23 species of common introduced terrestrial birds, mostly of European origin (Heather & Robertson 1996). Introduced birds differ from native birds as they co-evolved with mammalian predators in their native range and have life-history traits which reduce predation risk (Martin 1995; Briskie et al. 1999; Martin et al. 2000; Starling-Windhof et al. 2011). Hence introduced birds appear to benefit to a lesser extent from mammalian predator control compared to native species (Innes et al. 2010; Starling-Windhof et al. 2011). It is important to consider the effect of predator control on the entire avian community, including exotic species, as predator control may alter community composition.

Control or eradication of mammalian predators is widely recognised as necessary for both the protection of native bird species, and ecological restoration (Towns & Atkinson 1991; Atkinson 2001; Saunders & Norton 2001; Innes et al. 2010). Translocation of endangered birds to offshore islands free of mammalian predators has been the traditional method used for bird conservation in New Zealand (Clout & Saunders 1995; Saunders & Norton 2001; Parkes & Murphy 2003; Bellingham et al. 2010). More recently, there have been attempts to control multiple mammalian pest species on the New Zealand mainland, with species and ecosystem-focused restoration goals (Saunders & Norton 2001; Gillies et al. 2003). The Department of Conservation initiated the first projects, known as 'mainland islands', in 1995 and 1996 (Saunders & Norton 2001). Mainland islands have sustained intensive pest control aimed at reducing pests to low densities, and adjoin non-protected areas (Saunders & Norton 2001; Gillies et al. 2003). The first predator-proof fenced sanctuary in New Zealand was constructed in 1999, at Karori Sanctuary (now rebranded as Zealandia), Wellington (Speedy et al. 2007). Currently there are 17 fenced projects around New Zealand (Speedy et al. 2007; http://www.sanctuariesnz.org/projects, accessed 14 February 2012). Fenced sanctuaries differ from mainland islands as they are not subject to constant reinvasion by pests, allowing eradication or near-eradication of all mammalian pests (Speedy et al. 2007).

The purpose of this study was to determine whether the near-eradication of mammal pests from Maungatautari, a pest-proof fenced sanctuary in the Waikato and the largest fenced mainland sanctuary in New Zealand (http://www.sanctuariesnz.org/projects, accessed 14 February 2012), has altered the abundance and composition of the avifauna. To examine this five-minute bird counts from Maungatautari and a non-treatment site (Pirongia Mountain), were used. Counts were conducted by Landcare Research at both sites in 2002 and 2005, before pests were eradicated from Maungatautari, and in 2008 (by Landcare Research) and 2010 (by me) following pest eradication. Specifically, the following questions were asked:

1. Is there an effect of the near-eradication of pest mammals on the abundance of certain bird species at Maungatautari?
2. Do native species and exotic species show different responses to mammalian pest eradication?

2.2 Methods

2.2.1 Study sites

Maungatautari (38°01'S, 175°05'E) and Pirongia Forest Park (37°59'S, 175°05'E), are located in the Waikato Basin and are separated by approximately 35 km (Figure 2.1). Maungatautari is 3400 ha in size and the study site within Pirongia Forest Park, Pirongia Mountain (hereafter referred to as Pirongia), covers 13 600 ha. Maungatautari and Pirongia are highly eroded low-angle composite volcanic cones of a similar age (Kear et al. 1978). The soil groups of both sites are brown granular clays and yellow-brown loams (Arand et al. 1993). Mean annual temperatures are 13–14°C (Maunder 1970, 1974). The inland location of Maungatautari means it receives lower annual average rainfall (1400–1600 mm) than Pirongia (1775–3000 mm) and is cooler at equivalent altitudes (Maunder 1974; McQueen et al. 2004). While Pirongia (90–959 m a.s.l.) has a greater altitudinal range than Maungatautari (280–797 m a.s.l.), the vegetation at Pirongia and Maungatautari is similar in composition at equivalent altitudes (Burns & Smale 2002; Clarkson 2002). Both sites have lowland rimu-tawa (*Dacrydium cupressinum-Beilschmiedia tawa*) forests, which grade into upland forests composed predominantly of tawari (*Ixerba brexioides*), kamahi (*Weinmannia racemosa*) and tawheowheo (*Quintinia serrata*). Detailed descriptions of the vegetation at Maungatautari and Pirongia are provided by Cheeseman (1879), Gudex (1955, 1963), Burns and Smale (2002) and Clarkson (2002).

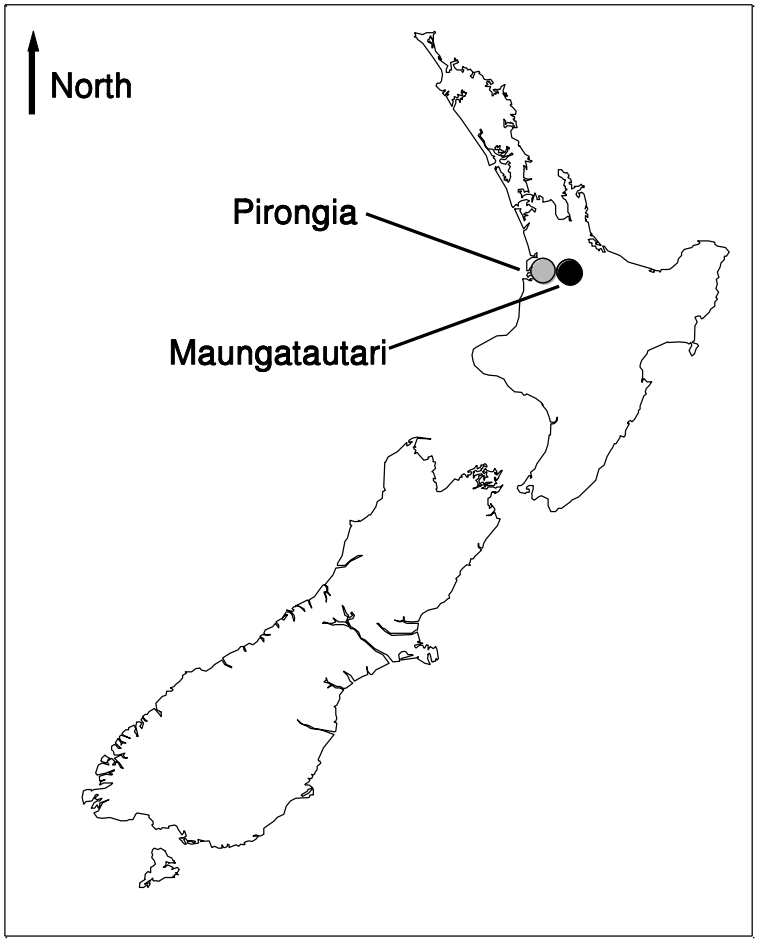

Figure 2.1: Locations of Maungatautari (treatment) and Pirongia (non-treatment).

2.2.2 Mammalian pest control

Prior to the construction of a mammalian pest-proof fence around Maungatautari in 2006, Maungatautari and Pirongia had similar histories of native flora and fauna loss and mammalian pest control (Innes et al. 2003; Fitzgerald et al. 2009). Both received aerial applications of 1080 (sodium monofluroacetate) targeted at possums before 2006. Pirongia received aerial 1080 in May 1996 and September 2002, while Maungatautari received aerial 1080 in June 1997 and July/August 2002 (Innes et al. 2003). In addition to possums, many non-target pests, such as ship rats (*Rattus rattus*), stoats (*Mustela erminea*) and feral cats, would have been killed by these 1080 operations (Murphy & Bradfield 1992; Innes et al. 1995, Gillies & Pierce 1999; Innes et al. 2003). Possums increase very slowly following large-scale poison operations and can take over ten years to recover, whereas rat and stoat numbers recover faster, in about 6 months (Murphy & Bradfield 1992; Innes et al. 1995; Murphy et al. 1999; Sweetapple et al. 2006). Controlling possums may result in greater

numbers of rats because of increased food availability (Sweetapple & Nugent 2007; Ruscoe et al. 2011).

Pirongia was most recently treated with aerial 1080 in July 2007, excluding an area subject to pest control by the Pirongia Te Aroaro o Kahu Restoration Society (PRS). The 1080 drop resulted in a residual trap catch rate of 0.42% (0.42 possums caught per 100 traps set) (M. Lewis, Department of Conservation, pers. comm.). The PRS initiated pest control over an area of 250 ha in 2006, targeting primarily rats using the toxin Pindone. If possums are detected they are trapped or poisoned with cyanide (C. St. Pierre, PRS, pers. comm.). Pest control efforts increased to 350 ha in 2008, and 715 ha during 2010 and early 2011 (C. St. Pierre, PRS, pers. comm., Figure 2.2). Bait stations are filled with poison baits from August to October each year, and post-operation rat tracking indexes show this method successfully reduces rats to low levels during the breeding season of most bird species (Heather & Robertson 1996; C. St. Pierre, PRS, pers. comm.).

At Maungatautari in 2004, the Maungatautari Ecological Island Trust (MEIT) built two small pest-proof fenced enclosures and eradicated mammalian pests from within them as a pilot for the main mountain eradication. These pilot enclosures have been considered free of mammalian pests since April 2005 (35 ha enclosure) and July 2006 (65 ha enclosure) (Speedy et al. 2007). In August 2006, a 47 km long mammalian pest-proof fence was built around most of the forested area on Maungatautari, totalling 3400 ha. Aerial application of brodifacoum-laced bait to eradicate mammalian pest species began in November 2006 within the fenced area on the main mountain. Further applications were made in December 2006 and June-July 2007 (Speedy et al. 2007). Residual mice (*Mus musculus*) were targeted using additional applications in 2008 (Fitzgerald et al. 2009). The first poisoning operations would have killed most of the mammalian pests (Fitzgerald et al. 2009). At the time of the bird counts in 2008, bird species had had at least one and a half breeding seasons without any (or at least greatly reduced) mammalian predators (Fitzgerald et al. 2009). By the December 2010 bird counts, low numbers of mice, rabbits (*Oryctolagus cuniculus*) and hares (*Lepus europaeus*) were the only mammalian pests left on Maungatautari (P. Quinn, MEIT, pers. comm.).

2.2.3 Bird counts

The avifauna at Maungatautari and Pirongia is representative of forest birds common to the Waikato region, and bird species present at Pirongia were similar to those at Maungatautari prior to pest eradication (Innes et al. 2003). Five-minute bird counts were used as an index of relative bird abundance at Maungatautari and Pirongia, using the methods described by Dawson and Bull (1975). Five-minute bird counts provide only an index of abundance, rather than a measure of

absolute density (Murphy & Kelly 2001; Innes et al. 2003). Counts measure changes in bird conspicuousness, which is assumed to be a close surrogate for actual abundance or density (Anderson 2001). However, counts are influenced by factors other than true bird abundance, such as observer variables, environmental conditions and species characteristics (Dawson & Bull 1975; Rosenstock et al. 2002). Despite these weaknesses, five-minute bird counts are the best available estimate of bird abundances at Maungatautari and Pirongia and are adequate for the purpose of this research.

Both sites had five-minute bird counts made during the pre-eradication period in 2002 and 2005, and following pest eradication counts were repeated in 2008 and 2010. Landcare Research conducted bird counts in 2002, 2005 and 2008 (Innes et al. 2003, 2006; Fitzgerald et al. 2009). Permission has been obtained from Landcare Research to use these data in my thesis. I made counts in 2010, using methods replicating those used by Landcare Research to make results comparable.

Bird counts were conducted at count stations located along access tracks (count lines) at Maungatautari and Pirongia, with 4–11 stations located along each count line (Figures 2.2 and 2.3). At both sites the count lines followed ridgelines. Where possible, stations at the two sites were placed at similar altitudes to increase comparability between sites (Innes et al. 2003). In all years, 36 bird count stations were used at Maungatautari and 34 count stations were used at Pirongia, except in 2008 when there were only 26 count stations at Pirongia. Count stations were separated by time (15 minutes at a steady walking pace), rather than distance, to allow Landcare Research to use a second indexing method that required a 30-minute survey interval (Innes et al. 2003). The stations were marked physically and using GPS, to ensure the same area was counted in each count year. Counts along each count line were always performed in the same order. Each station was visited twice on different days in each counting year. In 2002, 2005 and 2008, to remove observer differences, two separate observers spread their counting effort evenly between treatment and non-treatment sites and counted each station (Innes et al. 2003, 2006; Fitzgerald et al. 2009). In these years, variation in day effects between the treatment and non-treatment sites, such as weather, were minimised by undertaking equal numbers of counts on the same days at both locations (Innes et al. 2006). In 2010, I made all counts, alternating daily between treatment and non-treatment sites. In 2010 all stations were counted once before being recounted a second time, so any change in my counting ability should be shared evenly between Maungatautari and Pirongia. While daily weather may have varied in 2010, large-scale weather patterns should have been distributed evenly between treatment and non-treatment sites. Prior to beginning counts I was trained in the count method by John Innes and Neil Fitzgerald from Landcare Research who were involved in the previous counts, so I could calibrate my counts with theirs.

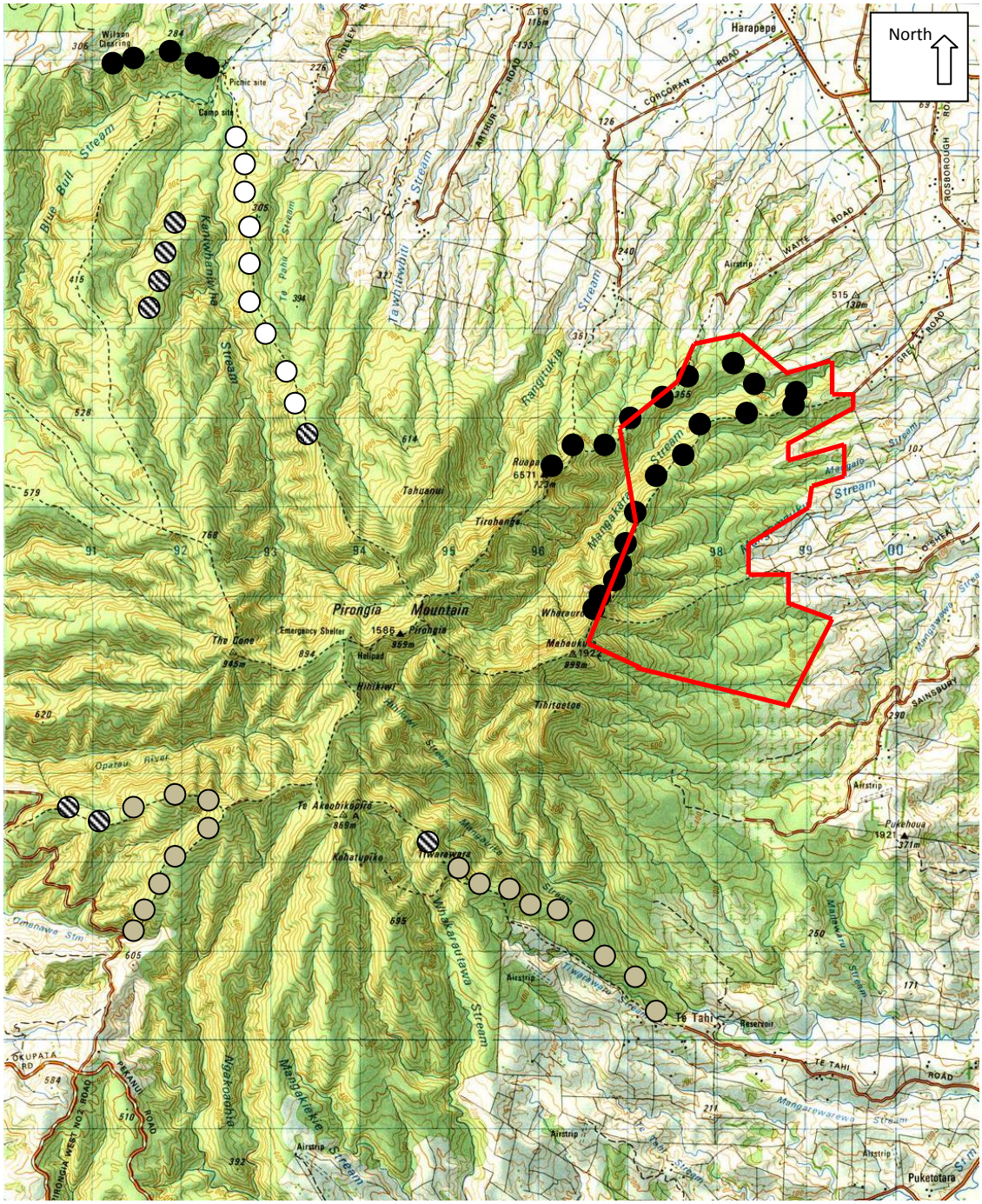

Figure 2.2: Locations of five-minute bird count stations on Pirongia Mountain. Twenty-five stations (black markers) were only used in 2002 and 2005, these count stations were replaced by new count stations in 2008 (grey markers). A further eight new stations were created in 2010 (striped markers) and nine stations were used in all years (open markers). The area enclosed within the red lines indicates the 715 ha of pest control conducted by the Pirongia Te Aroaro o Kahu Restoration, as of December 2010 - July 2011, see text for details. Base map sourced from NZMS 260 series, blue grid squares are equivalent to 1x 1 km. After figure 2 in Fitzgerald et al. (2009, page 7).

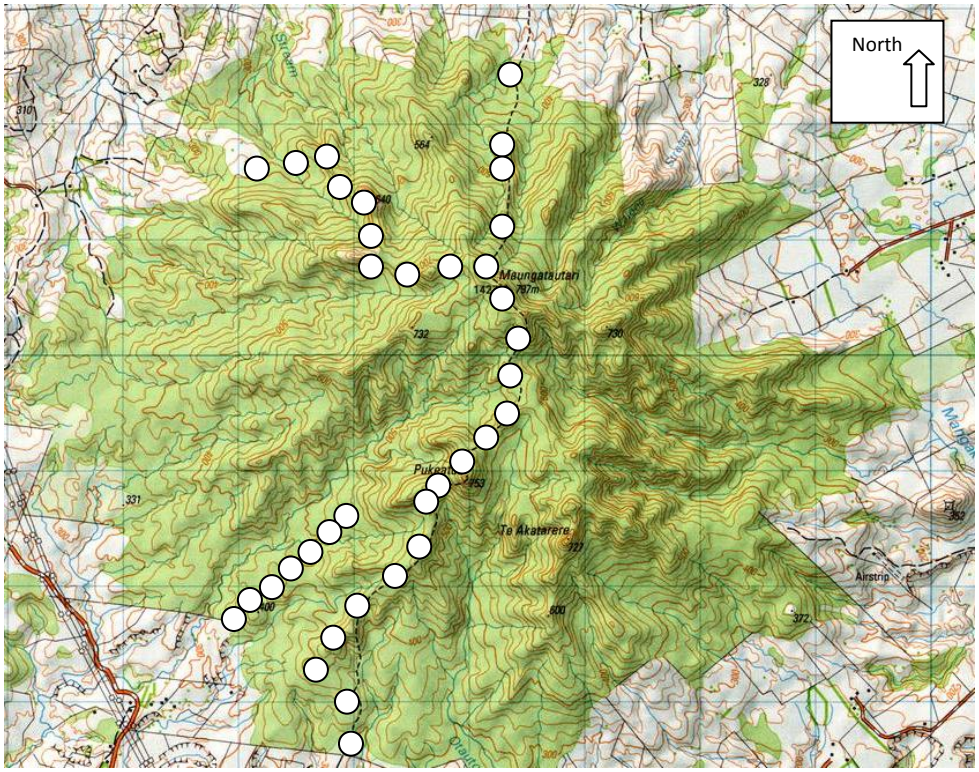

Figure 2.3: Locations of five-minute bird count stations on Maungatautari (open markers). All stations were counted in 2002, 2005, 2008 and 2010. Base map sourced from NZMS 260 series, blue grid squares are equivalent to 1 x 1 km. After figure 1 in Fitzgerald et al. (2009, page 6).

During counts, over a five-minute period, all birds seen and/or heard within an estimated 100 m radius of a stationary observer were recorded. Counts were made in fine weather, between two hours after sunrise to two hours before sunset, thus avoiding dawn and dusk periods of increased conspicuousness (Dawson & Bull 1975). Counts were conducted during the breeding season in late November and December, when most bird species are conspicuous and dispersed on breeding territories (Spurr & Powlesland 2000; Innes et al. 2003). Birds were only counted if there was a visual or auditory cue of their presence (Dawson & Bull 1975). Birds flying into or over the count area during the five-minute period were counted; as long as they were judged to belong to the vegetation type (e.g. seabirds were not counted). Within each count, no bird knowingly was counted twice to avoid overestimation of abundance (Dawson & Bull 1975). If a bird was initially heard calling from one location and then later another bird of the same species was heard calling from another location, it was assumed a different individual, unless it was apparent that the first bird travelled to the second location (Dawson & Bull 1975). As bellbirds, tui and kereru have species-specific noisy wing beats their movements can be tracked to some extent. Details specific to each count year are summarised below.

In 2002, three observers from Landcare Research conducted counts between 19 November and 6 December. The mean distance between stations was 350 m (Innes et al. 2003). In 2005, Landcare Research performed bird counts between 13 and 30 December. Pest fence location at Maungatautari and track closure at Pirongia meant that two stations were slightly re-located at each site. Four observers conducted the counts and mean distance between count stations remained at 350 m (Innes et al. 2006).

In 2008, Landcare Research used the same count stations at Maungatautari. However, track closure on Pirongia resulted in the abandonment of 5 stations, and intensive pest control by PRS over 350 ha of Pirongia caused a further 20 stations to be lost due to becoming unsuitable for non-treatment counts (Fitzgerald et al. 2009). To replace these stations, Landcare Research established 17 new count stations on Pirongia and 8 at another non-treatment site, Te Tapui Scenic Reserve (Fitzgerald et al. 2009, Figure 2.3). Counts from Te Tapui were not included in my analysis, thus in 2008 there were only 26 count stations at Pirongia. Mean distance between stations increased to 360 m. Five observers conducted the counts between 3 and 23 December (Fitzgerald et al. 2009).

In 2010, all counts were conducted between 1 and 30 December. Eight new stations were established at Pirongia to increase the number of count stations there. Four stations were placed on a disused track on the northern side of the mountain, and the three existing count lines were lengthened by adding a total of four further stations at their ends (Figure 2.2). All other count stations were the same as used by Landcare Research in 2008. The mean distance between counts remained 360 m.

2.2.4 Statistical analysis

The five-minute bird counts at Maungatautari and Pirongia detected a total of 32 bird species (19 native and 13 exotic) during the four count years. Counts from 2010 are presented in this chapter and for a summary of counts by Landcare Research in 2002, 2005 and 2008, refer to Fitzgerald et al. (2009, their table 1). There were sufficient data to run analysis over the four count years for 12 species (nine native and three exotic) individually, and mean counts for those species are presented here. Counts of 23 species were combined to examine changes in the total abundance of native and exotic species (see below for details).

All analyses were carried out using the "lme4" package (Bates et al. 2011) in R (version 2.14.1, R Development Core Team 2011). The Landcare Research dataset lacked zero counts; that is, if a particular species was not detected during a five-minute count then there was no record of that species for that count. Prior to analysis, data from Landcare Research were reshaped in R to include

all zero counts. This meant that all species had a data point for each five-minute bird count at a count station during each count year. My 2010 data already contained zero counts. The two datasets were combined in R to allow analysis over the four count years.

Generalised linear mixed models (GLMMs) were used to examine the effects of mammalian pest eradication from Maungatautari on each of the 12 species and the total abundance of native and exotic species. GLMMs allow analysis of data with non-normal error distribution and hierarchical random effects (grouping in both time and space in this case) (Crawley 2007). Due to the count nature of the data I specified poisson error distribution (and the associated log link), with the number of individuals of a particular species counted as the response. Count stations nested within count lines were included as random effects for all models.

A complication arose from only one observer making the counts in 2010, and that observer not having counted in any of the other count years. Ideally an observer term would be fitted as a random effect, allowing for observer differences. Inspection of the data suggests that some observers counted consistently higher or lower than others. Because only one observer made counts in 2010, fitting an observer term alters year trends for species which only show an increase in 2010 (e.g. bellbirds and kereru), as this increase may either be a true increase or an observer effect. Hence, observer was not included as a random effect, but it should be noted that the increase in counts of bellbirds and kereru may be caused by an observer effect rather than a year effect.

Statistical analyses tested how mean bird counts changed through time and if changes through time were different at Maungatautari and Pirongia. Initially Pirongia was to be used as a non-treatment comparison to Maungatautari, allowing changes in counts that were similar between sites to be attributed to factors other than pest control, such as weather and food availability. A significant site by year interaction would indicate an effect of pest eradication at Maungatautari on bird abundances. However, pest control at Pirongia during the course of the study (aerial 1080 and pest control by the PRS) reduced the validity of Pirongia as a non-treatment site, as changes observed at Pirongia may also be related to pest control. Therefore, either a site by year interaction or a significant change in abundance over time at Maungatautari is considered an indication of an effect of pest control at Maungatautari. This weakness in analysis due to a lack of a pure non-treatment site is one that has also been a problem in other studies (e.g. Langham 2010).

For each bird species a maximal model was constructed that initially included site, year (as a variate, but rescaled so than 2002 was 2 and 2005 was 5, and so on), and their interaction as fixed effects. Year was fitted as a variate to look for long term trends rather than fluctuations in abundance caused by a single good or bad year. Models were simplified by backward selection to

obtain final models. Akaike information criterion (AIC) values were used to examine the effect of deleting each variable from the maximal model. AIC provides a measure of model fit while accounting for the number of parameters used in the model; lower relative values of AIC indicate a more accurate model fit (Crawley 2007). Models were simplified until the removal of a variable increased the AIC value; the model with the lowest AIC value was chosen as the final model. Variables which were nearly significant (P = < 0.10) and whose removal resulted in a higher AIC score were retained in the final model as this analysis was exploratory.

For example, the R code for bellbirds was:

Bellbird.glmer <- glmer (bellbird ~ site + yeartrend + site:yeartrend + (1|countline/countstation), data = all.count.data, subset=(site!="Te Tapui"), family = poisson)

Secondly, changes in the total abundance of all native and all exotic species over time were examined, similar to Innes et al. (2010). Species were classed as native (native and endemic species) or exotic using the classifications provided in Heather and Robertson (1996). For each species group the total number of individuals counted during each five-minute count was used as the response. As for the analysis of individual species, year (as a variate), site and their interaction were fitted as fixed effects and count stations were nested within count lines as random effects. Species which were only counted during one count year could not be included in the analysis, as two or more years of data are needed to estimate change between years. Species excluded from the analysis were harrier (*Circus approximans*), falcon (*Falco novaeseelandiae*), morepork (*Ninox novaeseelandiae*), pukeko (*Porphyrio porphyrio*), takahe (*Porphyrio hochstetteri*), dunnock (*Prunella modularis*), goose (*Anser anser*), ring-necked pheasant (*Phasianus colchicus*) and starling (*Sturnus vulgaris*). These species were counted at very low levels and their exclusion made little difference to the total abundance (<0.05 birds counted per five-minute count in each year). Models were simplified in the same manner as for the analysis of individual species.

2.3 Results

Five-minute bird counts in December 2010 detected a total of 26 bird species (Table 2.1). Tui were the most common species counted, followed by grey warblers. Five species were recorded only at Maungatautari and three species only at Pirongia (Table 2.1), however these species were counted at low numbers and are mostly known to be present at both sites (Fitzgerald et al. 2009), except for takahe and riflemen. Takahe were introduced to Maungatautari in 2006 (C. Smuts-Kennedy, MEIT, pers. comm.) but riflemen have not been detected there.

Table 2.1: Mean number (and standard error in brackets) per five minute count of each bird species detected by five-minute bird counts at Maungatautari (MTT) and Pirongia (PIR) in December 2010. The total number of birds counted at both sites is shown. Birds are listed in decreasing order of total counts.

		Mean number per 5MBC		
Species	**Scientific name**	**MTT**	**PIR**	**Total**
Tui	*Prosthemadera novaeseelandiae*	4.19 (0.24)	1.82 (0.14)	426
Grey warbler	*Gerygone igata*	1.51 (0.14)	1.57 (0.12)	216
Tomtit	*Petroica macrocephala*	1.42 (0.11)	1.06 (0.11)	174
Chaffinch	*Fringilla coelebs*	1.26 (0.13)	0.82 (0.10)	147
Silvereye	*Zosterops lateralis*	0.90 (0.12)	1.04 (0.13)	136
Shining cuckoo	*Chrysococcyx lucidus*	1.40 (0.10)	0.44 (0.08)	131
Kereru	*Hemiphaga novaeseelandiae*	0.81 (0.12)	0.47 (0.09)	90
Fantail	*Rhipidura fuliginosa*	0.64 (0.09)	0.49 (0.11)	79
Blackbird	*Turdus merula*	0.75 (0.09)	0.34 (0.07)	77
Bellbird	*Anthornis melanura*	0.83 (0.09)	0.24 (0.06)	76
Kingfisher	*Halcyon sancta*	0.29 (0.07)	0.12 (0.04)	29
Rosella	*Platycercus eximius*	0.26 (0.07)	0.09 (0.04)	25
Magpie	*Gymnorhina tibicen*	0.07 (0.04)	0.18 (0.05)	17
Goldfinch	*Carduelis carduelis*	0.17 (0.06)	0.04 (0.03)	15
Greenfinch	*Carduelis chloris*	0.14 (0.06)	0 (0)	10
Whitehead	*Mohoua albicilla*	0.07 (0.04)	0.04 (0.03)	8
Myna	*Acridotheres tristis*	0.04 (0.03)	0 (0)	3
Rifleman	*Acanthisitta chloris*	0 (0)	0.04 (0.03)	3
Welcome swallow	*Hirundo neoxena*	0.03 (0.03)	0.01 (0.01)	3
Yellowhammer	*Emberiza citronella*	0.01 (0.01)	0.03 (0.02)	3
Paradise duck	*Tadorna variegata*	0.01 (0.01)	0.01 (0.01)	2
Pheasant	*Phasianus colchicus*	0 (0)	0.01 (0.01)	1
Pukeko	*Porphyrio melanotus*	0.01 (0.01)	0 (0)	1
Songthrush	*Turdus philomelos*	0 (0)	0.01 (0.01)	1
Starling	*Sturnus vulgaris*	0.01 (0.01)	0 (0)	1
Takahe	*Porphyrio hochstetteri*	0.01 (0.01)	0 (0)	1

2.3.1 Trends over time

Tui, chaffinches (*Fringilla coelebs*) and bellbirds showed significant increases over years at both Maungatautari and Pirongia (Table 2.2, Figure 2.4). These increases were similar at both sites, as shown by non-significant site by year interactions. Counts of tui, chaffinches and bellbirds were significantly lower at Pirongia (before pest eradication from Maungatautari and throughout the study) as indicated by a significant effect of site. Counts of kereru increased at Maungatautari and Pirongia during the counting period and there was no significant effect of site or the site by year interaction on counts (Table 2.2, Figure 2.4).

Only counts of shining cuckoos (*Chrysococcyx lucidus*) and kingfishers (*Halcyon sancta*) had significant site by year interactions (i.e., indicate an effect of pest eradication at Maungatautari only) (Table 2.2). Shining cuckoos at Pirongia increased only slightly between 2002 and 2010, whereas at Maungatautari shining cuckoos increased by 233% between 2002 and 2010. Kingfishers very slightly increased at Maungatautari over count years, while they decreased at Pirongia (Figure 2.4). Tomtits (*Petroica macrocephala*) had a marginally non-significant site by year interaction ($P = 0.070$, Table 2.2), indicating that while both sites had increasing trends over years the increase in abundance may have been greater at Maungatautari than at Pirongia.

Counts of silvereyes (*Zosterops lateralis*), fantails (*Rhipidura fuliginosa*) and grey warblers were similar at both sites and showed declining trends over count years (Table 2.2). Eastern rosellas (*Platycercus eximius*) also had declining trends (marginally non-significant, $P = 0.055$, Table 2.2) at both sites and counts were lower at Pirongia than at Maungatautari (again marginally non-significant, $P = 0.088$, Table 2.2).

There was a significant effect of site on counts of blackbirds (*Turdus merula*) with lower counts at Pirongia than Maungatautari, and there was no effect of year at both sites ($z = 0.818$, $P = 0.413$), indicating there was no directional trend in counts of blackbirds during the counting period.

Analysis of the total abundance of native and exotic species over years indicates that the two groups of species showed different trends over years (Figure 2.5, Table 2.3). Native species showed no significant main effect of site, but there was a significant positive main effect of year with total abundance increasing over time, there was also a significant site by year interaction indicating that the increase in abundance over time occurred more rapidly at Maungatautari than Pirongia (Figure 2.5, Table 2.3). Exotic species were significantly less abundant at Pirongia than Maungatautari (Figure 2.5, Table 2.3). Counts of exotic species showed no trend in counts over years at either site ($z = 0.369$, $P = 0.712$).

Table 2.2: Parameter estimates, standard error, z statistics and *P*-values of minimal adequate poisson GLMMs for 12 bird species, testing the effects of site, year and their interaction on counts at Maungatautari and Pirongia. Year is in the models as a variate (rescaled so that 2002 is 2 and 2005 is 5, etc.). Count stations nested within count lines were included as random effects in each model. Significant effects are in bold.

Species	Fixed effects	Estimate	Std. Error	z value	Pr(>|z|)
Tui	(Intercept)	0.3562	0.0965	3.6920	<0.001
	Site(Pirongia)	-0.7216	0.0914	**-7.8980**	**<0.001**
	Yeartrend	0.1053	0.0104	**10.1360**	**<0.001**
Grey warbler	(Intercept)	0.5482	0.0774	7.0830	<0.001
	Yeartrend	-0.0224	0.0114	**-1.9610**	**0.050**
Silvereye	(Intercept)	0.7417	0.0807	9.1880	<0.001
	Yeartrend	-0.0784	0.0124	**-6.3110**	**<0.001**
Tomtit	(Intercept)	-1.1685	0.2172	-5.3800	<0.001
	Site(Pirongia)	0.3657	0.3200	1.1430	0.253
	Yeartrend	0.1569	0.0225	**6.9880**	**<0.001**
	Site(Pirongia):Yeartrend	-0.0676	0.0373	-1.8100	0.070
Chaffinch	(Intercept)	-0.4622	0.1583	-2.9210	0.003
	Site(Pirongia)	-0.3579	0.1521	**-2.3530**	**0.019**
	Yeartrend	0.0511	0.0173	**2.9590**	**0.003**
Fantail	(Intercept)	-0.3270	0.1884	-1.7360	0.083
	Yeartrend	-0.0453	0.0193	**-2.3410**	**0.019**
Shining cuckoo	(Intercept)	-1.5870	0.2131	-7.4470	<0.001
	Site(Pirongia)	0.1320	0.3380	0.3900	0.696
	Yeartrend	0.1869	0.0260	**7.1850**	**<0.001**
	Site(Pirongia):Yeartrend	-0.1336	0.0443	**-3.0130**	**0.003**
Blackbird	(Intercept)	-0.2720	0.0933	-2.9140	0.004
	Site(Pirongia)	-0.8773	0.1548	**-5.6680**	**<0.001**
Bellbird	(Intercept)	-0.9906	0.2190	-4.5240	<0.001
	Site(Pirongia)	-0.9400	0.2292	**-4.1010**	**<0.001**
	Yeartrend	0.0483	0.0237	**2.0350**	**0.042**
Kereru	(Intercept)	-1.9861	0.2352	-8.4450	<0.001
	Yeartrend	0.1083	0.0260	**4.1620**	**<0.001**
Rosella	(Intercept)	-1.1656	0.3040	-3.8340	<0.001
	Site(Pirongia)	-0.5938	0.3480	-1.7060	0.088
	Yeartrend	-0.0581	0.0304	-1.9150	0.055
Kingfisher	(Intercept)	-1.4723	0.2846	-5.1740	<0.001
	Site(Pirongia)	0.5933	0.4016	1.4770	0.140
	Yeartrend	0.0057	0.0388	0.1480	0.883
	Site(Pirongia):Yeartrend	-0.1414	0.0619	**-2.2830**	**0.022**

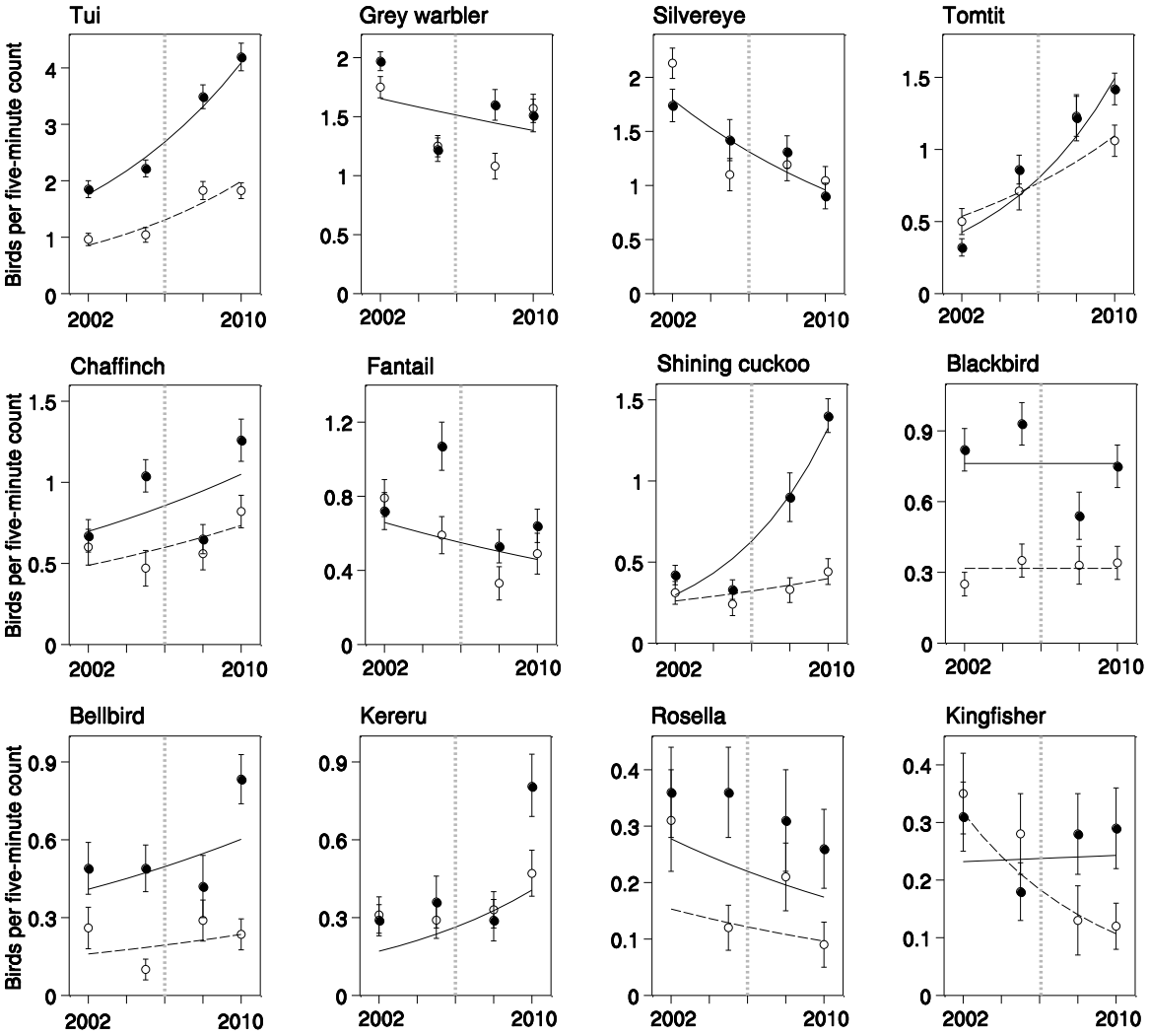

Figure 2.4: Mean five-minute bird counts (± SEM) of 12 species at Maungatautari (filled circles) and Pirongia (open circles) in November/December 2002, 2005, 2008 and 2010. Lines are fitted from the minimal adequate GLMM for each species (solid black line, Maungatautari; black dashed line, Pirongia; solid black line only, same trend at both sites). Vertical grey dashed lines indicate the completion of the pest-proof fence around Maungatautari at the end of 2006. Note the different scales of the Y axes.

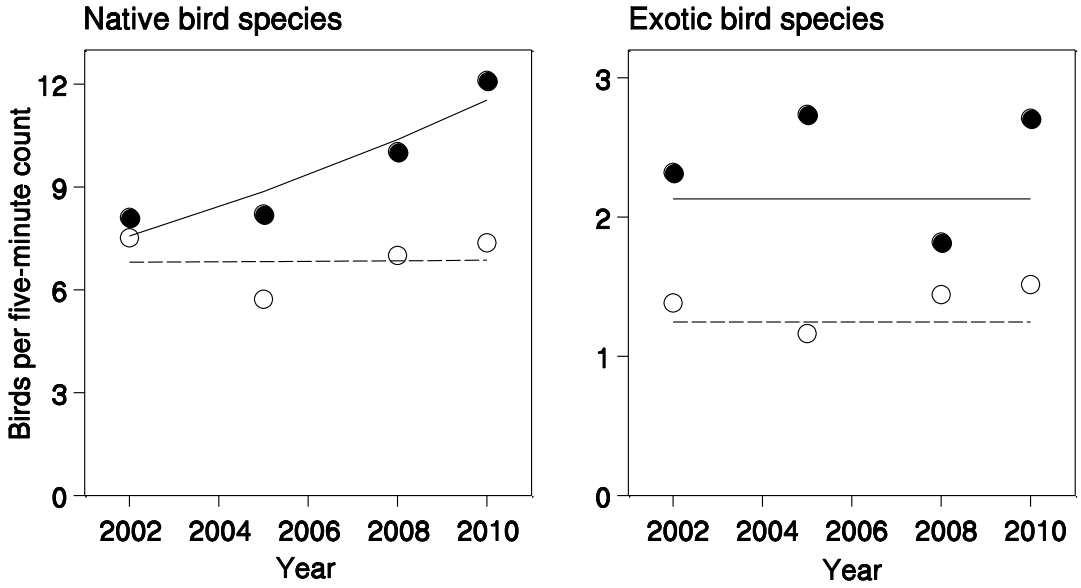

Figure 2.5: Average total abundance of native and exotic bird species at Maungatautari (filled circles) and Pirongia (open circles) over count years. Trend lines are fitted from poisson GLMMs (Maungatautari black and Pirongia dashed) (see Table 2.3). Note different scales on Y axes.

Table 2.3: Parameter estimates, standard error, z statistics and *P*-values of minimal adequate poisson GLMMs for the total abundance of native and exotic species, testing the effects of site, year and their interaction on counts at Maungatautari and Pirongia. Year is in the model as a variate (rescaled so that 2002 is 2 and 2005 is 5 etc.). Count stations nested within count lines were included as random effects in each model. Significant effects are in bold.

Species Group	Fixed Effects	Estimate	Std. Error	Z value	Pr(>|z|)
Native species	(Intercept)	1.9186	0.0488	39.290	<0.001
	Site(Pirongia)	-0.0072	0.0743	-0.100	0.923
	Yeartrend	0.0527	0.0064	**8.200**	**<0.001**
	Site(Pirongia):Yeartrend	-0.0496	0.0103	**-4.830**	**<0.001**
Exotic species	(Intercept)	0.7559	0.0904	8.364	<0.001
	Site(Pirongia)	-0.5356	0.1242	**-4.313**	**<0.001**

2.4 Discussion

Ten of the 12 bird species examined, and native species in general, showed a significant change in abundance following mammalian pest control at Maungatautari. Of the six species which showed an increase in abundance, three of these, tui, bellbirds and kereru, are important pollinators and/or dispersers.

There are a number of considerations to be taken into account whilst drawing conclusions from the data, these include: lack of replication of sites, a weak non-treatment site (Pirongia), and insufficient years of count data. It cannot positively be said that changes in bird numbers are due to the attempted pest eradication at Maungatautari, as this study lacks replication (having only one treatment site and one non-treatment site) or supporting evidence such as improved nest success. Additionally, Pirongia is a weak non-treatment site due to the pest control work which occurred there during the same time period as pest eradication at Maungatautari. The 1080 drop in July 2007 over most of Pirongia resulted in low abundances of possums (M. Lewis, Department of Conservation, pers. comm.), and probably also reduced the abundance of ship rats and stoats during at least the early part of the 2007-2008 bird breeding season (Murphy & Bradfield 1992; Innes et al. 1995; Murphy et al. 1999; Sweetapple et al. 2006). Furthermore yearly pest control by PRS at Pirongia, since 2006, has successfully reduced rats to low levels during the breeding season of most birds (0 – 2 % tracking rates in December, following control during August to October of each year (C. St. Pierre, PRS, pers. comm.). Rats are a significant predator of native bird species (Atkinson 1973; Moors 1983; Elliott et al. 1996; Innes et al. 1996; Anderson & Craig 2003) and eradication of rats has increased the abundance of some native bird species (Miskelly & Robertson 2001; Graham & Veitch 2002). Although the pest control by PRS is over a relatively small area (715 ha in 2010), which was not used for bird counts by this study, this area may provide a source of juvenile birds for the rest of the mountain. Hence, I have considered it reasonable to look at changes at Maungatautari alone as an indication of pest removal. Studies examining effects of mammalian pest control on bird populations on offshore islands frequently lack non-treatment comparisons as it is difficult to find suitable sites (e.g. Miskelly & Robertson 2001; Graham & Veitch 2002; Spurr & Anderson 2004). On the mainland the lack of non-treatment sites is increasingly becoming a problem for people wanting to examine the effects of mammalian pest control (e.g. Fitzgerald et al. 2009; Langham 2010), as many areas are now receiving some form of pest control whether it is by the Department of Conservation, Animal Health Board or community groups.

Despite have four sets of counts spread over eight years, the present data set is limited by a lack of count years. Having only two sets of counts prior to pest eradication and two sets following pest eradication only allows for fitting of linear trends in abundance through count years. There may be more complex trends in the data with potential 'steps' in abundance after pest eradication and 'short-term trend' responses following pest eradication. Additional years of bird count data could indicate more complex patterns of population change. For example, Elliott et al. (2010) examined bird counts between 1974 and 1984 and between 2002 and 2005, at Nelson Lakes. This large dataset allowed fitting of different or similar trends in abundance between the two sets of counts. The results showed that population trends were variable and complex between the two periods (Elliott et al. 2010). There may also be lag periods in population responses. For instance, kokako populations only really began to increase after four years of mammalian pest control at Mapara (Innes et al. 1999). Further counts conducted by Landcare Research in the future will allow for a more complete analysis of changes in bird abundance at Maungatautari.

However, despite these limitations, the results indicate that the attempted pest eradication at Maungatautari may have positively affected the abundance of tui, tomtits, chaffinches and shining cuckoos, and possibly bellbirds and kereru. Not all species appear to have benefitted, with counts of grey warblers, silvereyes, fantails and rosellas declining over count years at Maungatautari. The results of my study are generally consistent with those of other studies, giving more confidence in my findings.

2.4.1 Increases in abundance of kereru, tui and tomtits

Kereru, tui and tomtits appear to have benefitted from the near-eradication of pests from Maungatautari. As previously mentioned in the methods, the increase in kereru may be affected by observer effects, as an increase was only found in the 2010 counts and this increase occurred at both sites. However, we would expect kereru populations, along with tui and tomtit populations, to increase following predator removal from Maungatautari. All three species are vulnerable to nest predation by ship rats and possums (Clout et al. 1995; Brown 1997; Innes et al. 2004; Innes et al. 2010), and ship rats may also eat nesting adult tomtits (Innes et al. 2010). Previous studies have shown control of ship rats and possums positively benefits kereru populations, as indicated by decreases in nest predation and population increases (Clout et al. 1995; Innes et al. 2004). Furthermore, contrasts of kereru abundance between areas with intensive pest control and areas with lesser control indicate kereru reach higher abundances in the areas with more extensive control (Smith & Westbrooke 2004; Baber et al. 2009).

Tui can have several clutches of two to four eggs each breeding season (Higgins et al. 2001), allowing rapid population recovery following predator control. Counts of tui increased following control of ship rats and possums at Motatau in Northland (Innes et al. 2004), and with integrated pest management in the Landsborough Valley (O'Donnell & Hoare 2012). Tui also increased, but not significantly, following eradication of kiore (*Rattus exulans*) from Tiritiri Matangi Island (Graham & Veitch 2002). However, tui may have declined following eradication of kiore and Norway rats (*Rattus norvegicus*) from Kapiti Island (Miskelly & Robertson 2001).

Tomtits have been found to be more abundant at sites with higher levels of pest management compared to sites with less pest management (Smith & Westbrooke 2004; Baber et al. 2009), but surprisingly there is little evidence of tomtits showing positive changes in abundance in response to pest management. For example, tomtits declined in the Landsborough Valley despite long-term intensive pest management (O'Donnell & Hoare 2012) and showed no population level response to control of ship rats and possums at Motatau (Innes et al. 2010). O'Donnell and Hoare (2012) suggested the decline observed at Landsborough may be because of increased competition from other bird species, or because tomtits feed close to or on the ground, increasing their vulnerability to predation. Perhaps the intensive level of pest control such as that at Maungatautari, where only mice remain, may be required for tomtit populations to increase.

2.4.2 Unexpected slow increase in bellbirds

Bellbirds were expected to benefit from mammalian pest eradication at Maungatautari (Innes et al. 2003). Yet bellbirds showed a decrease in the 2008 counts, 1.5 breeding seasons after the fence was completed. The 2010 counts indicate bellbirds may now be starting to increase (although this could be an observer effect). Previous studies show bellbirds have high nest failures due to predation in forest areas without predator control (Poirot 2004; Kelly et al. 2005), and respond well to pest control. Kelly et al. (2005) found after one season of stoat control at Craigieburn in South Island, bellbirds detected per five-minute count increased by 79%. Similarly, stoat trapping in Fiordland increased local bellbird densities (Efford & Morrison 1991) and significant increases in bellbirds were found over a 10 year period of mammalian pest control in the Landsborough Valley (O'Donnell & Hoare 2012). Following kiore eradication from Tiritiri Matangi Island, a 91% increase in bellbird numbers was observed (Graham & Veitch 2002). However, native plantings which were established during this period and associated increased habitat and food supply may have enhanced this effect (Graham & Veitch 2002).

Two possible reasons for the delayed increase of bellbirds at Maungatautari are outlined below. Firstly, it could be due to imbalanced sex ratios, with more males present than females. Populations

of bellbird at sites without mammalian predators may have a male population bias, due to greater survival of males as they are larger than and competitively dominant over female bellbirds (Craig et al. 1981; Sagar & Scofield 2006). For example, on Aorangi Island in the Poor Knights Islands group, 68% of bellbirds caught in mist nests, near the only fresh water source on the island, outside the breeding season, were males (Sagar & Scofield 2006). Sites with mammalian predators may also have a male population bias due to greater predation of female bellbirds. Only female bellbirds incubate the eggs and do the majority of brooding the nestlings (Sagar 1985; Heather & Robertson 1996; Anderson & Craig 2003), making them more vulnerable to predatory mammals than male bellbirds (Anderson & Craig 2003). For example, few kokako pairs attempted to breed at Mapara when predator control first started, as most pairs were male-male due to a lack of females in the population, mostly likely caused by predation of females on the nest (Innes et al. 1999).

Secondly, inter-specific competition from tui may be important in limiting the recovery of bellbird populations (Anderson & Craig 2003; Fitzgerald et al. 2009). Tui are at reasonably high densities at Maungatautari, both species are nectar-feeding and tui aggressively displace bellbirds from food resources (Craig et al. 1981; Craig 1985). To prove bellbird numbers are limited by tui it would be necessary to demonstrate that there is a common limiting resource between the species (Fitzgerald et al. 2009).

2.4.3 Decline of exotic and biogeographically recent birds

Innes et al. (2003) predicted that not all bird species would be "winners" with mammalian pest eradication from Maungatautari and some species such as exotic and biogeographically recent native birds (e.g., fantails, silvereyes and grey warblers) would be "losers", and show decreasing trends, possibly due to increased competition from endemic bird species (Innes et al. 2010).

Of the three individual exotic species examined in this study, only eastern rosellas showed an indication of declining trends at Maungatautari. Chaffinches had significantly increasing trends, while blackbirds showed no trend over time. These three exotic species have previously shown different responses to mammalian pest control at different sites. Both eastern rosellas and chaffinches increased at Motatau following control of multiple pest species (Innes et al. 2004). However, chaffinches decreased during 10 years of mammalian pest control in the Landsborough Valley (O'Donnell & Hoare 2012), they also decreased slightly (but not significantly) following kiore eradication from Tiritiri Matangi Island (Graham & Veitch 2002). Blackbirds showed a small (non-significant) increase in abundance following kiore eradication from Tiritiri Matangi Island (Graham & Veitch 2002) and counts of blackbirds decreased during pest control in the Landsborough Valley (O'Donnell & Hoare 2012). No change in apparent density of blackbirds was

found after a 15-year period at Pureora, irrespective of pest management (Smith & Westbrooke 2004).

Fantails, grey warblers and silvereyes are all common and widespread on the New Zealand mainland (Robertson et al. 2007) and may have benefitted from the clearance of forest and increased shrub and forest edge habitats (Heather & Robertson 1996). However, they less common in intact forest communities without mammalian pests (Diamond & Veitch 1981; Heather & Robertson 1996; Innes et al. 2003). These species had declining trends at Maungatautari and Pirongia, similar to trends observed at other sites following mammalian pest control or eradication. Silvereyes and grey warblers declined on Tiritiri Matangi Island following kiore eradication (Graham & Veitch 2002). On Cuvier Island after goats and cats were eradicated and domestic stock fenced from the forest, a dense understory developed and grey warblers declined and silvereyes virtually disappeared (Diamond & Veitch 1981). Fantails and grey warblers may have declined after possum eradication from Kapiti Island (Innes et al. 2010), and silvereyes declined after kiore and Norway rats were eradicated (Miskelly & Robertson 2001). Grey warblers decreased in abundance following mammalian pest control at three mainland islands (Te Urewera National Park, Trounson Kauri Park and Motatau in Northland) (Innes et al. 2010). The observed declines in abundance of grey warblers, fantails and silvereyes may be related to changes in forest composition (Diamond & Veitch 1981; Graham & Veitch 2002) and/or increased competition from other native species, most likely for food (Innes et al. 2010). However, despite declines in some of the biogeographically recent natives, my analysis showed that native birds as a group still increased over time at Maungatautari.

Changes in the total abundance of native and exotic species in response to mammalian pest control found by this study are similar to those found by Innes et al. (2010). The total abundance of native species increased more rapidly over count years at Maungatautari compared to at Pirongia. Innes et al. (2010) found that native bird species at four mainland islands (two podocarp-broadleaved forests in North Island and two beech forests in South Island) showed increases in total abundance following the commencement of pest control. In contrast, the total abundance of exotic species showed no clear trend in abundance over years at Maungatautari and Pirongia. Similarly at the same mainland sites, Innes et al. (2010) found that exotic bird species showed no significant trends with time after mammalian predator control.

The different responses of exotic and native species to mammalian predator control may be partly due to differences in their vulnerability to predation. Exotic birds evolved with mammalian predators in their native ranges. Conversely, many native New Zealand birds (although not all, e.g. silvereyes and fantails) evolved without mammalian predators and lack adaptations to reduce

predation risk (Moors 1983; Holdaway 1989; Lovegrove 1996; O'Donnell 1996), although some native birds may alter certain behaviours in response to mammalian predation (e.g., bellbirds, Massaro et al. 2008). Starling-Windhof et al. (2011) found that exotic and native bird species benefitted differently from mammalian predator control during the breeding season, with native species benefiting from increased nest success significantly more than exotic species. Predator control did not significantly improve nest success of silvereyes (classed by Starling-Windhof et al. (2011) as introduced), dunnocks or blackbirds, but did improve nest success of song thrush (*Turdus philomelos*) (Starling-Windhof et al. 2011). All four native species examined, fantails, robins (*Petroica australis*), bellbirds and grey warblers, had increased nest success at the predator control site and this was significant for bellbirds and grey warblers (Starling-Windhof et al. 2011).

2.4.4 Additional effects of reduced mammalian pests

Mammalian pest eradication from predator-proof fenced sanctuaries is a complete ecosystem manipulation. Bird species are not only released from mammalian predation but also from competition from mammals for foods, such as fruits, seeds, foliage and invertebrates (Miskelly & Robertson 2001; Graham & Veitch 2002; Spurr & Anderson 2004; Sweetapple & Nugent 2007; Innes et al. 2010). The removal of mammalian seed predators and herbivores may also alter the vegetation structure (Diamond & Veitch 1981; Graham & Veitch 2002; Wilson et al. 2006). For example at Maungatautari, toropapa, a shrub which has nectar-producing flowers and fruit eaten by birds, increased in abundance following pest eradication. The relative importance of reduced predation, decreased competition from mammals, and vegetation changes on bird abundance are unknown. In order to determine their relative roles it would be necessary to remove mammal species slowly (one at a time or ecologically similar groups, e.g. herbivores) and examine the resulting changes in bird populations (Innes et al. 2003). Alternatively, detailed demographic studies may provide some insight (Wilson et al. 1998; Innes et al. 1999; Innes et al. 2010).

2.4.5 Effects of species reintroductions

Current abundances of bird species at Maungatautari are likely to change in the future. The removal of mammalian predation as a limiting factor means that other limiting factors such as intra-specific and inter-specific competition for limited resources will come become more important (Innes et al. 2010). Additionally, species re-introductions will further alter bird abundances once new species become established and increase. Seven species have currently (at time of writing in March 2012) been reintroduced to Maungatautari, including robins, whiteheads (*Mohoua albicilla*) and hihi (*Notiomystis cincta*) (C. Smuts-Kennedy, MEIT, pers. comm.). At present these species are at low abundances. At Te Urewera National Park the observed decline in grey warblers may have been

due to increased competition from whiteheads (Jones 2000 cited by Innes et al. 2010). This effect could be seen at Maungatautari in the future as whitehead numbers increase. Reduced abundance of grey warblers may then stop the current increasing trend seen for shining cuckoos, as shining cuckoos are nest parasites of grey warblers (Heather & Robertson 1996). Both grey warblers and shining cuckoos are uncommon on Little Barrier and Kapiti Islands (Diamond & Veitch 1981; Innes et al. 2003). Similarly, Miskelly and Robertson (2001) suggested that the decline of tomtits on Kapiti Island following rat eradication was related to increased competition from robins which increased during the same period.

This chapter has examined whether the near-eradication of mammalian pests has altered bird abundances at Maungatautari. Of the bird species examined, tui, bellbirds and silvereyes are both important pollinators and seed dispersers (Clout & Hay 1989; Kelly et al. 2006), while kereru and possibly blackbirds are also important seed dispersers (Clout & Hay 1989; Williams & Karl 1996; Kelly et al. 2006). All five species demonstrated similar changes in abundance at Maungatautari and Pirongia over the period pest eradication at Maungatautari; however, most are more abundant at Maungatautari than at Pirongia, indicating there are more birds at Maungatautari to provide plants with pollination and seed dispersal services. The following two chapters focus on what happens to the bird services provided to native plants at different bird densities. Chapter 3 will examine the density of key pollinators (tui, bellbirds and silvereyes) in 2010 only, to see what effect they are having on the pollination service received by *Fuchsia excorticata*. Chapter 4 will examine whether different densities of tui, bellbirds, silvereyes, blackbirds and kereru in 2010 are influencing the dispersal service received by *Fuchsia excorticata*, tawa (*Beilschmiedia tawa*) and miro (*Prumnopitys ferruginea*).

Chapter 3

Is it Possible to Restore Bird Pollination of *Fuchsia excorticata*?

3.1 Introduction

Bird mutualists provide plants with a range of services, including pollination and seed dispersal, which contribute significantly to maintaining plant populations and community dynamics (Kearns et al. 1998; Sekercioglu et al. 2004). However, the decline in range and density of bird species worldwide potentially places the ecosystem services that they provide at risk (Sekercioglu et al. 2004; Traveset & Richardson 2006).

Failure of either pollination or dispersal mutualisms could increase the risk of plant extinction (Bond 1994). Extinction risk is influenced by three factors: the likelihood of pollinator or disperser failure, the extent which reproduction depends on the mutualism (e.g. flowers require visits by pollinators or seeds require visits by dispersers), and the demographic importance of seeds (i.e. the population is seed-limited) (Bond 1994). When assessing the risk of mutualist failure it is important to establish the level of mutualist service received, and factors that influence this (Kelly et al. 2004). Sekercioglu et al. (2004) identified New Zealand as being particularly at risk of mutualism failure because New Zealand has a high proportion of bird pollinated and bird dispersed trees compared to other temperate regions (Lord 1999; Kelly et al. 2010), and the pre-human avifauna has been considerably altered (Holdaway 1999).

In New Zealand, tui (*Prosthemadera novaezelandiae*, Meliphagidae), bellbirds (*Anthornis melanura*, Meliphagidae) and silvereyes (*Zosterops lateralis*, Zosteropidae) are presently important pollinators (Craig et al. 1981; Kelly et al. 2006). Hihi (stitchbird *Notiomystis cincta*, Notiomystidae (Driskell et al. 2007)) would also have been important pollinators in the North Island before becoming restricted to offshore islands and few mainland sites to which they have been recently reintroduced (Craig et al. 1981; Kelly et al. 2006). Although no pollinating birds are thought to have become extinct (Atkinson & Millener 1991), all extant pollinating bird species, with the exception of silvereyes, have restricted distributions and/or densities compared to pre-human times. Before human arrival, bellbirds and tui were widespread throughout most of mainland New Zealand, as were hihi in North Island (Higgins et al. 2001). Bellbirds and hihi suffered dramatic declines during the 19th century, and by the late 1880s bellbirds were virtually absent from northern North Island and hihi only remained on Little Barrier Island (Buller 1877; Heather & Robertson

1996; Higgins et al. 2001). Tui also declined during the 19th century to a lesser extent (Higgins et al. 2001), they were lost from the Banks Peninsula in the 1960s (Wilson 2008) and remain rare in eastern South Island (Higgins et al. 2001). These declines coincided with the spread of ship rats (*Rattus rattus* Atkinson 1973) but are also related to habitat loss and more speculatively avian disease (Heather & Robertson 1996; Higgins et al. 2001). While bellbirds and tui have since increased on the mainland, they are more abundant on island bird sanctuaries (e.g., Diamond & Veitch 1981; Murphy & Kelly 2001), where abundances are probably most similar to pre-human densities (Castro & Robertson 1997).

Direct measurements of pollination services to plants show that mutualism failure is occurring for some plant species, presumably because of reduced bird densities and species (Robertson et al. 2008; Anderson et al. 2011). Comparisons of the bird-pollinated plant *Rhabdothamnus solandri*, between the New Zealand mainland where the sole pollinating birds are tui, to island bird sanctuaries where all endemic bird pollinators are abundant, show pollen-limited fruit set on the mainland but not on the islands (Anderson et al. 2006, 2011). *Peraxilla* mistletoes, *Sophora microphylla*, *Fuchsia perscandens* and *Fuchsia excorticata* are also frequently pollen-limited on the mainland (Robertson et al. 1999; Montgomery et al. 2001; Kelly et al. 2007; Robertson et al. 2008).

Removal of mammalian predators and corresponding increases in bird abundance indicates that predation by mammals is the current primary limiting factor of endemic forest birds on the New Zealand mainland (Innes et al. 2010). Control of mammalian pests is becoming increasingly prevalent, often attempting to restore whole communities (Saunders & Norton 2001). The Department of Conservation (DOC), during 1995 and 1996, initiated the first 'mainland islands' (Saunders & Norton 2001). These are areas with species and ecosystem-focused restoration goals, which have sustained intensive control of multiple pest species (Saunders & Norton 2001). Since 1999, predator-proof fenced sanctuaries have been constructed on the mainland, allowing eradication or near-eradication of mammalian pests (Speedy et al. 2007; Innes et al. 2012). Pest control or eradication not only benefits native bird species but also directly benefits native plant species by decreasing consumption of vegetative or reproductive parts (e.g., Cowan 1991; Sessions et al. 2001; Dijkgraaf 2002; Urlich & Brady 2005; Wilson et al. 2006).

Benefits of mammalian pest control to bird-plant mutualisms remain less well known. The only attempt aimed specifically at restoring a bird-plant mutualism in New Zealand is that of Kelly et al. (2005). They attempted to restore the pollination service to the pollen-limited mistletoe, *Peraxilla tetrapetala*, by trapping stoats (*Mustela erminea*) to enhance bellbird numbers, but were unsuccessful. However, it cannot be assumed that decreased (or improved) rates of pollination

and/or dispersal will have an effect at the population level, as plants may compensate for poor bird services using other strategies, such as longevity (Bond 1994).

The purpose of this study was to determine whether the control of mammalian pests indirectly restores the pollination service received by *Fuchsia excorticata*. To examine this, Maungatautari was chosen as a focal fenced sanctuary paired with a non-treatment site, Pirongia Mountain, which has a lower level of mammalian pest control. Additionally, data on pollination levels of *F. excorticata* from sites around New Zealand, with a range of predator-control levels, were examined.

Maungatautari is the largest predator-proof fenced sanctuary in New Zealand (Innes et al. 2012). The Maungatautari Ecological Island Trust (MEIT) has a goal to create a self-sustaining ecosystem, through the eradication of mammalian pests and reintroduction of endemic species that have been lost from Maungatautari (McQueen et al. 2004). At the time of the study six bird species, including hihi, had been reintroduced to Maungatautari (C. Smuts-Kennedy, MEIT, pers. comm.). Hence, Maungatautari has all of the key extant pollinating birds present.

Fuchsia excorticata has several features that make it an ideal candidate species to determine whether mammalian pest control is restoring pollination services. *Fuchsia excorticata* is bird pollinated. It is gynodioecious (plants are either females or hermaphrodites), and fruit production in hermaphrodites and especially females is frequently pollen-limited on the New Zealand mainland (Anderson et al. 2006; Robertson et al. 2008). *Fuchsia excorticata* appears to be seed-limited, indicating that pollen-limitation has consequences at the population level (Bell 2010). Additionally, pollen loads on *F. excorticata* stigmas are well correlated to fruit set, allowing rapid assessment of pollination mutualism service (Robertson et al. 2008).

This study had four objectives:

1. Determine the relative abundances of pollinating bird species at Maungatautari (treatment) and Pirongia (non-treatment).
2. Determine which bird species are visiting flowers of *F. excorticata* at Maungatautari and Pirongia.
3. Examine pollination levels of *F. excorticata* at Maungatautari and Pirongia.
4. Examine pollination levels of *F. excorticata* at sites around New Zealand with and without intensive mammalian pest control.

3.2 Methods

3.2.1 Study sites

Maungatautari (38°01'S, 175°05'E) is located in the Waikato Basin approximately 40 km southeast of Hamilton city. A 47 km long mammalian pest-proof fence has been built around 3400 ha of forest. Eradication of mammalian pest species from within the fenced area began in November 2006 using aerially applied brodifacoum-laced bait, with further applications in December 2006 and June-July 2007 (Speedy et al. 2007). The initial poisoning operations would have killed the majority of mammals (Fitzgerald et al. 2009). At the time of this study, in November and December 2010, the only mammalian pests remaining on Maungatautari were low numbers of mice (*Mus musculus*), rabbits (*Oryctolagus cuniculus*) and hares (*Lepus europaeus*) (P. Quinn, MEIT, pers. comm.).

Pirongia Forest Park (37°59'S, 175°05'E), 35 km west of Maungatautari, is the largest continuous forest remaining in the Waikato (Burns & Smale 2002) and is administered by DOC. The area used by this study, Pirongia Mountain (referred to hereafter as Pirongia), covers 13 600 ha. Mammalian predators are present at Pirongia although intermittent applications of aerial sodium monofluoroacetate (1080) are used to control brushtail possums (*Trichosurus vulpecula*). Pirongia was most recently treated in July 2007, resulting in a low residual trap catch rate of 0.42% (0.42 possums caught per 100 traps set) (M. Lewis, DOC, pers. comm.). Rats (ship rat *Rattus rattus*) and stoats, while most likely reduced in numbers by the poison operation, are expected to have recovered within a year (Murphy & Bradfield 1992; Innes et al. 1995; Murphy et al. 1999). The avifauna at Pirongia is representative of forest birds common to the Waikato region and similar to that at Maungatautari prior to pest eradication (Innes et al. 2003).

Both sites are volcanic in origin and although Pirongia has a greater altitudinal range (90–959 m a.s.l.) than Maungatautari (280–797 m a.s.l.); the sites have similar vegetation compositions at similar elevations. Vegetation changes attitudinally from lowland tawa (*Beilschmiedia tawa*) forests with emergent rimu (*Dacrydium cupressinum*), to upland forests composed predominantly of kamahi (*Weinmannia racemosa*), tawari (*Ixerba brexioides*) and tawheowheo (*Quintinia serrata*) (Burns & Smale 2002; Clarkson 2002). Gudex (1955, 1963), Burns and Smale (2002), Clarkson (2002) and McQueen et al. (2004), describe the landforms and vegetation of Maungatautari and Pirongia in detail.

3.2.2 Study species

Fuchsia excorticata (Onagraceae) is a long-lived endemic tree, which can grow to 13 m in height, and is found in lowland to subalpine forests throughout New Zealand (Poole & Adams 1963). It is a partially seral species which is later overtopped by other trees (Robertson et al. 2008), and is typically found near riverbanks, along forest margins and in disturbed habitats (Godley & Berry 1995). *Fuchsia excorticata* is a highly preferred food of possums, and heavy browsing by possums has caused dieback or local extinction throughout much of its range (Pekelharing et al. 1998; Sweetapple et al. 2004). The production and dispersal of viable seed is crucial for this species to persist because of herbivory by possums and its partially seral nature (Robertson et al. 2008).

Fuchsia excorticata is gynodioecious, and high fruit set is possible for both female and hermaphrodites (Robertson et al. 2008). Hermaphrodites are self-compatible and able to autonomously self when pollinators are absent (Godley 1955; Robertson et al. 2008). However, selfed offspring have lower fitness and suffer from cumulative inbreeding depression (Robertson et al. 2011). While sex ratios are variable between locations, hermaphrodites always outnumber females (Godley 1955; Robertson et al. 2008). Flowers of female plants are much smaller than those of hermaphrodites and produce less nectar (Delph & Lively 1985). Fruit production in hermaphrodites and especially in females is frequently pollen-limited (Robertson et al. 2008).

Elsewhere in New Zealand, the current key pollinators of *F. excorticata* are tui and bellbirds (Delph & Lively 1985; Kelly et al. 2006). The now extremely rare hihi would probably once have been an important pollinator (Godley & Berry 1995; Kelly et al. 2006). Silvereyes are often observed feeding on *F. excorticata* flowers but are primarily considered nectar robbers (Delph & Lively 1985; Robertson et al. 2008).

3.2.3 Five-minute bird counts

Five-minute bird counts, in December 2010, were used as an index of pollinating bird abundance at Maungatautari (treatment) and Pirongia (non-treatment), using standardised methodology described by Dawson and Bull (1975). All birds seen or heard within a 100 m radius of a stationary observer were recorded during a five-minute period. A total of 36 bird count stations at Maungatautari and 34 count stations at Pirongia were used, and each count station was counted twice. One observer made all counts, alternating daily between treatment and non-treatment sites. All stations were counted once before being counted a second time; hence, any change in the observer's ability should be spread evenly between sites. Pollinating birds were defined as tui, bellbirds, silvereyes and hihi. To determine if Maungatautari and Pirongia had different relative abundances of each

pollinating bird species, poisson generalised linear models (GLMs) were used in the statistical package R (version 2.14.1, R Development Core Team 2011). Each species was analysed separately using the sum of counts for that species at each count station to avoid pseudoreplication. Predictors were site, altitude, altitude-squared and first order interactions. The inclusion of altitude-squared allowed examination of whether altitude effects were linear or quadratic. Models were simplified using likelihood ratio tests in R (the 'anova(model1, model2)' command). Explanatory variables which did not significantly improve model fit were deleted from the maximal model, but site was always retained as that was of most interest. To obtain fitted means per five-minute bird count rather than per 10-minute count, estimates were divided by two.

3.2.4 Bird visitors to *Fuchsia excorticata* flowers

To identify bird visitors to *F. excorticata* flowers at Maungatautari and Pirongia, observations were conducted during November 2010. At each site, 10 observation stations were selected from which several flowering *F. excorticata* could be clearly viewed. A total of 75 minutes was spent in five 15-minute blocks at each station. Each station was only visited once per day. During an observation period, for each avian flower visitor, the bird species and visit duration in seconds was recorded, using 8 x 42 binoculars at a distance of 5–10 m. Additionally, the number of receptive flowers was estimated to provide a mean number of flowers present at that station across all observations. To spread observation efforts evenly across both sites during the flowering period and minimise the effect of large-scale weather patterns on bird activity, Maungatautari and Pirongia were visited on alternate days. Visitation rates were expressed as the number of seconds of bird activity per 100 flowers per hour for each bird species at an observation station, following Robertson et al. (2008). Non-parametric Wilcoxon rank sum tests in R were used to analyse visitation rates for each species, using observation stations as replicates. As silvereyes rob hermaphrodite flowers but pollinate the smaller female flowers (Delph & Lively 1985; Robertson et al. 2008), only visits to female flowers were included in analysis of this bird species.

3.2.5 Pollen loads at Maungatautari and Pirongia

To assess the level of pollination received by *F. excorticata* the quantity of pollen deposited on stigmas was scored visually. The amount of pollen received by stigmas is correlated with fruit set for both female and hermaphrodite plants, providing an indication of how well the pollination mutualism is working (Robertson et al. 2008).

At Maungatautari and Pirongia, in November 2010, the percentage of the yellow stigma covered with blue pollen was visually scored on a five-point scale: (0) 0%; (1) 1–5%; (2) 6–20%; (3) 21–

40%; and (4) 41–100%, using standardised methodology developed by the University of Canterbury and Landcare Research for the National Pollination Survey (http://www.biol.canterbury.ac.nz/pollination_survey/, accessed 12 September 2011). Plants were selected on the basis of having 10 or more accessible flowers in the early to mid-stage of flowering (as indicated by the green corolla). On each plant, 10 receptive flowers were selected haphazardly across multiple branches. Stigmas were inspected using a 10 x hand lens. Flowers that had been damaged by silvereye robbing or other means were not scored. Plants were scored for pollen loads on two dates two weeks apart. As open flowers last for approximately 11 days and are only receptive for the first five or so (Delph & Lively 1985, 1989), the two visits scored separate groups of flowers.

Females were less common than hermaphrodites, which limited the number of female plants scored for pollen loads. The same plants were scored on both visits, except those with too few flowers at the second visit and one that had died. In total, 21 hermaphrodites and 15 females at Maungatautari were scored at the first visit (18 + 11 at second visit), and 19 plus 6 at Pirongia (18 + 5 at second visit) were scored.

Robertson et al. (2008) first used this method to quantify pollination levels at seven sites across New Zealand. However, in their work a four-point scale was used. Pollen loads were classed as (0) none, (1) few, (2) some, or (3) abundant (Robertson et al. 2008). Robertson et al. (2008) determined that a pollen score index of 1.5 indicated good pollination service based on the relationship between pollen load and fruit set (Robertson et al. 2008). To examine whether having an extra pollen load class (0 to 4) would affect comparisons drawn between the two experiments, the classes of "3" and "4" in the data from this study were collapsed, as any scores of "4" were likely to have been scores of "3" in Robertson et al. (2008). The analysis was then rerun using the four-point scale. This made no difference to the conclusions compared to the original analysis. Thus, all analyses presented use the full five-point scale to match the National Pollination Survey.

To avoid pseudoreplication given the nested nature of the data (replicate flowers on replicate plants), analysis was performed using mean pollen scores per plant per visit. Mean pollen scores were analysed using an ANOVA in R. Plant (a unique code for each plant examined) was fitted as an error term, to account for repeated measurements of the same plant at the two visits. Predictors fitted were site, visit, plant sex and first-order interactions. All predictors are factors with two levels. Due to the non-orthogonal nature of the data, where unequal numbers of observations exist for each combination of factor levels, each term was placed last in the model to test for its significance (Type III adjusted sum of squares, Quinn & Keough 2002).

3.2.6 National Pollination Survey

The National Pollination Survey was established in 2007 to assess the status of bird-plant mutualisms in New Zealand, using volunteers to measure the pollination service received by *F. excorticata*, as an indicator species for mutualisms generally. The data presented here are from surveys conducted in spring/summer 2007, 2008, 2009, 2010 and 2011, at 68 sites around New Zealand from Whangarei to Stewart Island (Figure 3.1). At each site (or visit to a site), observers attempted to score 10 flowers on each of 10 hermaphrodite and five female plants using the five-point pollen load scale outlined above. Some sites had lower numbers of plants or fewer than 10 suitable flowers on a plant, in which case all plants present and up to 10 flowers per plant were examined. Data from Maungatautari and Pirongia in 2010 were included in the analysis, however greater than 10 hermaphrodite and five female plants were examined per visit (see above for further details). Sites had an average of 9.7 hermaphrodite trees (range 1-21) scored per visit and 4.4 female trees (range 0-15).

I used DOC conservancy areas (http://gis.doc.govt.nz/docgis, accessed 27 October 2011) to divide National Pollination Survey sites into three regions, roughly matching the four regions used by Murphy and Kelly (2001) but combining northern and southern North Island categories due to a low number of sites in the North Island. The three regions were North Island (all North Island DOC conservancies), Western South Island (Nelson-Marlborough, West Coast, Southland) and Eastern South Island (Otago, Canterbury), which is drier and has less forest and lower bird densities than Western South Island (Murphy & Kelly 2001). A separate "low-predator" category was used for low-predator sites (mammalian predator-proof fenced, islands or mainland islands), regardless of their geographic region. The low-predator category was used to examine whether *F. excorticata* at sites that have intensive pest management and/or an absence of mammalian predators, and hence probably higher native bird densities, have better pollination service. The three geographic regions and the low-predator category will now be referred to as 'regions'. There were seven North Island sites (including Pirongia in 2010), 28 western South Island, 15 eastern South Island and 18 low-predator sites. The 18 low-predator sites were at 10 locations; fenced sanctuaries (Maungatautari, Bushy Park near Wanganui, Zealandia in Wellington, and Orokonui near Dunedin), unfenced mainland sites with intensive predator control (Boundary Stream in Hawkes Bay, Rotoiti Nature Recovery Project at Nelson Lakes, and Eglinton Valley) and islands lacking some major predators (Matakohe Island in Whangarei Harbour, Steward Island, and D'Urville Island in the Marlborough Sounds). D'Urville Island has stoats and kiore (*Rattus exulans*), but not possums, ship rats or Norway rats (*Rattus norvegicus*) (King 2005). Similarly, Stewart Island has ship rats, Norway rats, kiore and possums, but not stoats (Harper 2009). Matakohe Island is free of possums, stoats, kiore and ship rats; however, Norway rats remain (King 2005).

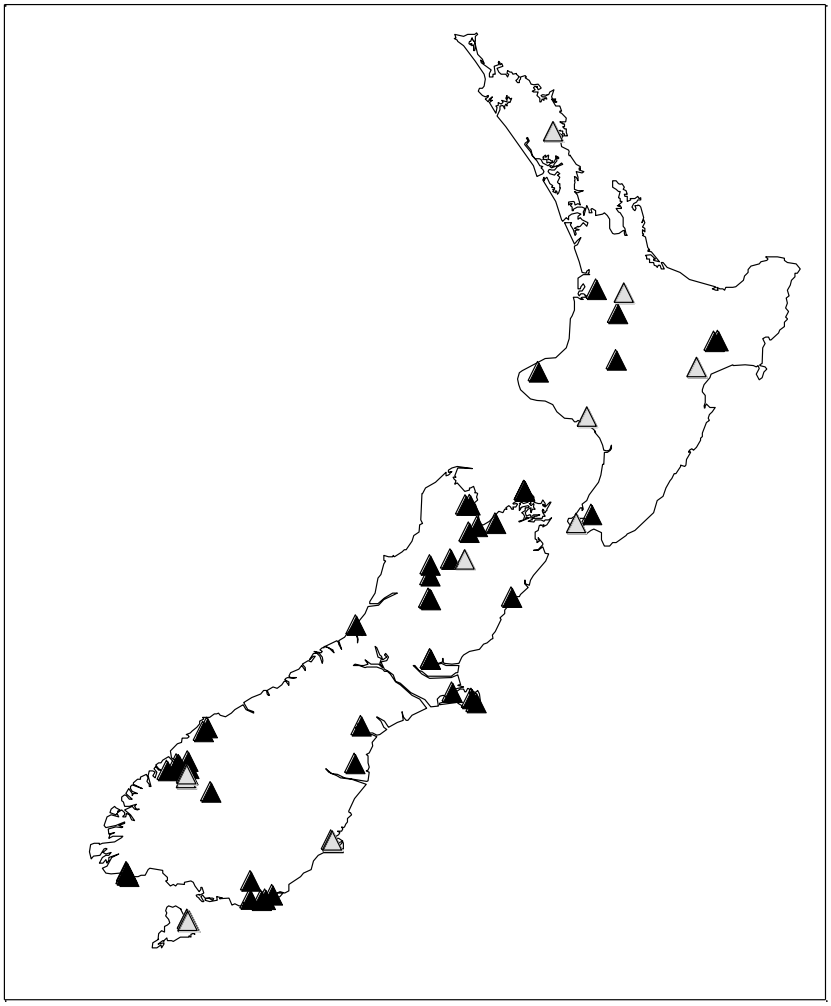

Figure 3.1: Locations of National Pollination Survey sites in all years (2007, 2008, 2009, 2010 & 2011). Grey triangles with black borders are sites classified as low-predator (fenced, island and mainland island) sites, and black triangles are all other sites. Some sites are obscured by other sites (e.g., there are actually 6 sites on Stewart Island).

Most sites were surveyed using a single visit during the flowering season. However, five sites were surveyed twice within a given year (two dates separated by 2–4 weeks) and 10 were surveyed in more than one year (7 sites surveyed in 2 years and 3 sites in 3 years). One site, Maungatautari, was surveyed once in 2008 and twice in 2010. Data were analysed using linear mixed models in the "lme4" package (Bates et al. 2011) in R. Models were fitted using maximum likelihood and Gaussian error distribution. The use of maximum likelihood allows comparison of models with different fixed effect structures (Crawley 2007). As for the Maungatautari data, a mean pollen score was calculated for each plant (the response variable), and then region, plant sex, number of flowers scored and first order interactions were fitted as fixed effects. To account for multiple measurements at sites within and between years, random effects were fitted for year and visit

nested within site. The maximal model was simplified using backward selection to obtain final models. The effect of removing each fixed effect from the maximal model was compared using likelihood ratio tests. Fixed effects which did not significantly improve model fit were removed from the final model. As models with Gaussian error distribution in the lme4 package do not provide significance testing, P values were generated using the "pvals.fnc" function in the "languageR" package (Baayen 2011), which uses Markov Chain Monte Carlo (MCMC) simulations. Confidence intervals (95%) were calculated using MCMC in the "arm" package (Gelman et al. 2011). To extract the confidence intervals from the minimal adequate model the full data set was used but the number of flowers term was excluded from the model.

3.3 Results

3.3.1 Five-minute bird counts

Five-minute bird counts showed that tui and bellbirds, which are key pollinators, were significantly more abundant at Maungatautari than Pirongia (Figure 3.2, Table 3.1). Silvereye abundance was similar at both sites (Figure 3.2, Table 3.1). The altitude term influenced counts of the three species, the effects of altitude were linear rather than quadratic (Table 3.1). Counts of tui and bellbirds increased with increasing altitude, while silvereye counts decreased with increasing altitude. There was a near significant site by altitude interaction for bellbird counts indicating that the increase in abundance with altitude may have occurred more rapidly at Pirongia than Maungatautari. Altitude effects may also be related to changes of conspicuousness caused by time of day, as counts were always performed with increasing altitude throughout the day (although most changes are related to increased conspicuousness at dawn and dusk, and stations were not counted during these periods). Consequently it is not clear whether these are truly effects of altitude or effects of time of day (or some combination of both).

At Maungatautari, although hihi are known to be present and were occasionally observed while walking between bird count stations, they were not detected by the five-minute counts. Hihi are found predominately on the lower slopes of Maungatautari, especially near the northern and southern gates where birds were initially released, and less frequently on the ridges where most of the five-minute bird counts were conducted. At Pirongia hihi are not present.

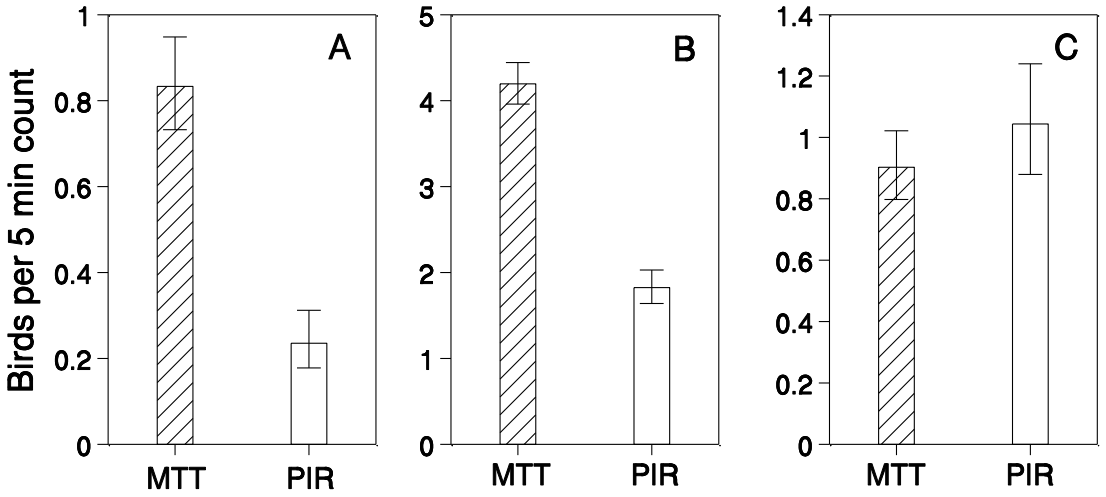

Figure 3.2: Mean number (± SEM) of bellbird (A), tui (B) and silvereye (C) per five-minute count at Maungatautari (MTT) and Pirongia (PIR) in December 2010. Note different scales on Y-axes. Values are fitted from poisson GLMs with site as the only predictor.

Table 3.1: The effect of site, altitude and their interaction on the abundance of bellbird, tui and silvereye at Maungatautari and Pirongia, from minimal adequate poisson GLMs. Significant effects are in bold type.

Species	Model	d.f.	Deviance	P(>|Chi|)	% Explained
Bellbird	Site	1	24.68	**<0.001**	25.16
	Altitude	1	6.59	**0.010**	6.71
	Site:Altitude	1	2.98	0.084	3.04
	Residual	66	63.84		
Tui	Site	1	66.88	**<0.001**	47.05
	Altitude	1	5.23	**0.022**	3.68
	Residual	67	70.023		
Silvereye	Site	1	0.72	0.397	0.61
	Altitude	1	17.72	**<0.001**	15.15
	Residual	67	98.52		

3.3.2 Bird visitation to *Fuchsia excorticata* flowers

Visitation rates by all pollinating birds to *F. excorticata* flowers were 3.6 times higher at Maungatautari than Pirongia, and this difference was significant (Figure 3.3). At Maungatautari, tui made the most visits (13), but bellbirds which only made nine visits had longer visits and so provided more seconds of visit per 100 flowers per hour. Hihi were also recorded visiting flowers (three visits), and five visits by silvereyes were seen but these were to hermaphrodite plants so are not included here. At Pirongia, silvereyes made three visits and provided 59.7% of all pollinating

time on flowers, while the three tui visits provided the remaining 40.3% of visitation time (Figure 3.3). Seven silvereyes also visited hermaphrodite plants at Pirongia but these are not included. Using Wilcoxon sum rank tests, the visitation rate was significantly higher at Maungatautari for bellbirds (W = 80, $P = 0.006$; n = 10, 10 for each test) and all birds combined (W = 22, $P = 0.029$) but not for tui (W = 61, $P = 0.328$), silvereyes (W = 45, $P = 0.368$) or hihi (W = 65, $P = 0.078$). At Maungatautari, aggression between pollinators was observed; tui displaced feeding bellbirds and hihi, and bellbirds displaced hihi. At Pirongia, no aggression was observed.

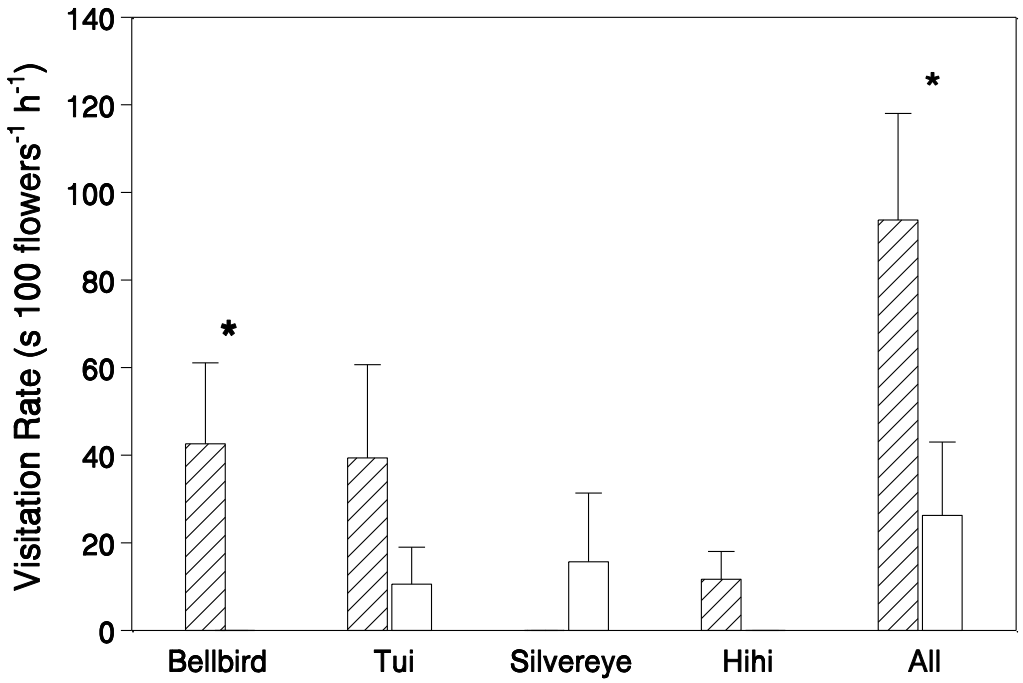

Figure 3.3: Visitation rates of pollinating birds to *F. excorticata* flowers (mean seconds of bird activity per 100 flowers per hour + SEM) at Maungatautari (hashed bars) and Pirongia (open bars). Visits by silvereyes to hermaphrodite flowers are excluded. Asterisks indicate significant differences in visitation ($P < 0.05$ = *, $P < 0.001$ = **), see text.

3.3.3 Pollen loads at Maungatautari and Pirongia

Fuchsia excorticata pollen scores were significantly higher at Maungatautari than Pirongia for both female and hermaphrodite plants (Figure 3.4). The ANOVA showed significant effects of site and the interaction between site and sex (Table 3.2), with the lowest pollen scores found for females (which cannot self-pollinate) at Pirongia (which had lower bird numbers). Pollen scores did not vary significantly between visits. Pollen scores of both female and hermaphrodite plants at Pirongia

are below the level of pollination (pollen score index of 1.5), which indicates good pollination service based on the relationship between pollen load and fruit set (Robertson et al. 2008), whereas both sexes at Maungatautari received good pollination service.

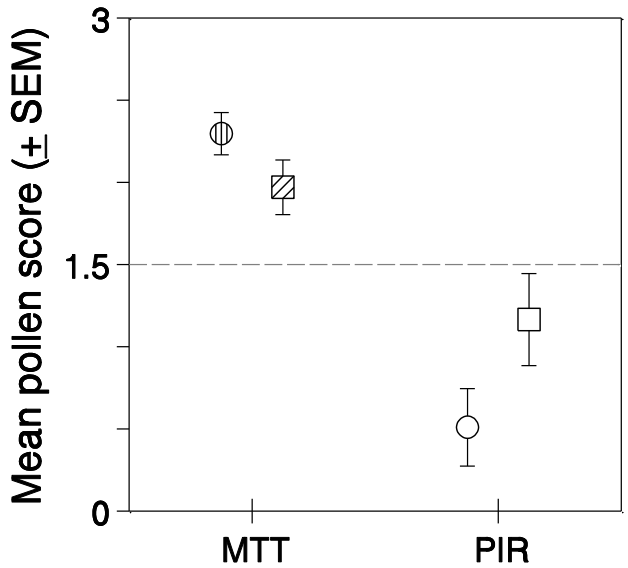

Figure 3.4: Fitted values for pollen scores of female (circles) and hermaphrodite (squares) plants at Maungatautari (MTT) and Pirongia (PIR). A pollen score index of 1.5 (shown by the dotted line) indicates good pollination service based on the relationship between pollen load and fruit set (Robertson et al. 2008).

Table 3.2: Split-plot analysis of variance of *F. excorticata* mean pollen scores. The significance of each predictor was calculated when it was last in the model. Significant effects are in bold type.

	Df	**SS**	**MS**	**F**	***P***
Error: plant					
Site	1	31.32	31.32	**59.587**	**<0.001**
Sex	1	0.01	0.01	0.018	0.893
Sex:site	1	4.59	4.59	**8.735**	**0.005**
Residual	54	28.39	0.53		
Error: within					
Visit	1	1.16	1.16	3.595	0.064
Visit:sex	1	0.37	0.37	1.130	0.293
Site:visit	1	0.26	0.26	0.804	0.374
Residual	49	15.86	0.32		

3.3.4 National Pollination Survey

The model which best described the National Pollination Survey data had plant sex, region, number of flowers scored and the sex by region interaction as fixed effects (Table 3. 3). Interactions between sex and number of flowers, and number of flowers and region did not improve model fit so were removed. Pollen scores were higher for hermaphrodite plants than female plants in each region (Table 3.3, Figure 3.5). Females at low-predator sites had significantly higher pollen scores than for females in any other region (Table 3.3, Figure 3.5). Hermaphrodite plants had fairly high pollen scores in all regions, except for North Island, and only hermaphrodites at North Island sites had significantly lower pollen scores than those at low-predator sites when examined alone (Table 3.4). Further sampling of *F. excorticata* pollen scores is needed from the North Island region, as only seven sites were sampled there. The number of flowers scored had a significant effect on pollen scores of both female and hermaphrodite plants with higher pollen scores on plants that had more flowers sampled (Table 3.3), perhaps because birds are attracted more to large floral displays.

Table 3.3: Parameter estimates, standard error, t statistics and *P*-values of a linear mixed model testing the effects of region, plant sex, number of flowers examined and the interaction between region and sex on mean pollen scores. Sites, visit nested within sites and years were included as random effects. Significant effects are in bold.

Fixed effects	**Estimate**	**Std. error**	**t value**	***P****
Intercept (Females at low-predator sites)	1.0877	0.3567	3.049	0.002
Region(Eastern SI)	**-0.9665**	**0.2618**	**-3.692**	**<0.001**
Region(North Island)	**-0.8878**	**0.3296**	**-2.694**	**0.007**
Region(Western SI)	**-0.7076**	**0.2237**	**-3.163**	**0.002**
Sex(Hermaphrodite)	**0.3083**	**0.0779**	**3.956**	**<0.001**
Number of flowers	**0.0637**	**0.0277**	**2.303**	**0.021**
Region(Eastern SI):Sex(Hermaphrodite)	**1.0705**	**0.1281**	**8.356**	**<0.001**
Region(North Island):Sex(Hermaphrodite)	0.2808	0.1589	1.767	0.078
Region(Western SI):Sex(Hermaphrodite)	**0.3439**	**0.1036**	**3.321**	**0.001**

**P*-values generated using MCMC, see methods for details

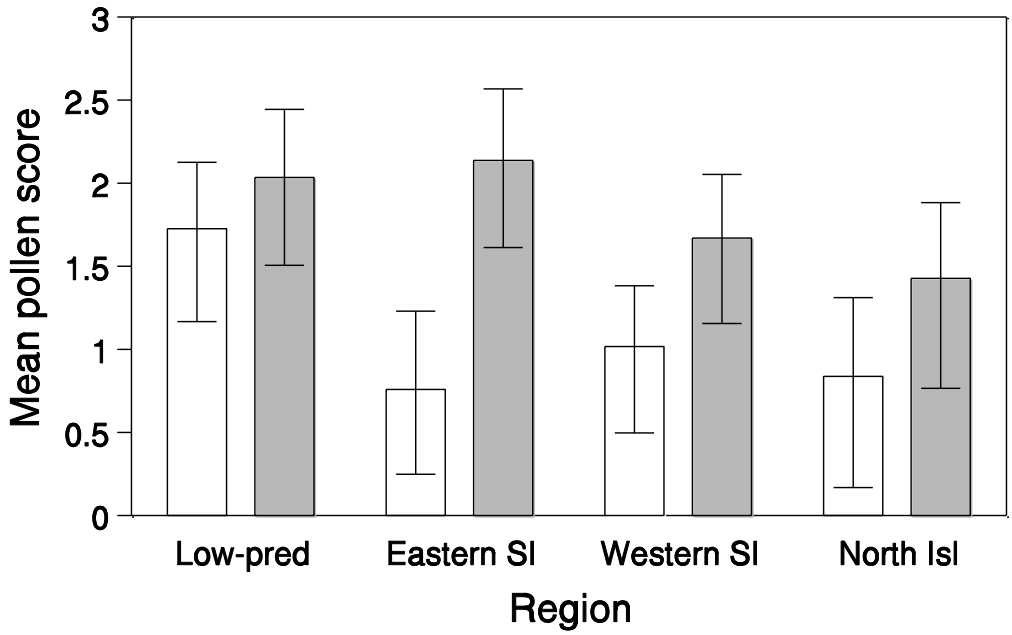

Figure 3.5: Fitted values for pollen scores of female (open bars) and hermaphrodite (grey bars) plants within each region, 95% confidence intervals shown. Means are fitted from the linear mixed model presented in Table 3.3, each parameter (e.g. low-predator females) was calculated with the 'number of flowers' term equalling 10, and confidence intervals were generated using a model with all the data included but without a term for the number of flowers.

Table 3.4: Parameter estimates, standard error, t statistics and *P*-values of a linear mixed model testing the effect of region on mean pollen scores of hermaphrodite plants only. Sites and years were included as random effects. Visit nested within sites was not included as a random effect in this model as it explained very little variance (<0.001) and its exclusion made no difference to model fit (AIC and likelihood ratio tests) or model parameter estimates. Significant effects are in bold.

Fixed effects	**Estimate**	**Std. error**	**t value**	***P****
Intercept (Low-predator sites)	2.0571	0.2316	8.884	<0.001
Region(Eastern SI)	0.0654	0.2735	0.239	0.792
Region(North Island)	**-0.7607**	**0.3098**	**-2.455**	**0.015**
Region(Western SI)	-0.4158	0.2347	-1.772	0.087

**P*-values generated using MCMC

3.4 Discussion

Results from this study are consistent with the idea that higher abundances of key pollinating birds at Maungatautari have improved the pollination service to *F. excorticata*. All parameters examined (pollinating birds, visitation and pollen loads) were higher at Maungatautari compared to Pirongia. Furthermore, data from the National Pollination Survey suggest that low-predator sites also improved the pollination service to female *F. excorticata*.

3.4.1 Status of pollination service

Godley (1979) and Clout and Hay (1989) considered bird pollination to be unimportant in the New Zealand flora. However, a growing body of literature challenges this view (e.g., Ladley & Kelly 1995; Anderson 2003; Newstrom & Robertson 2005; Anderson et al. 2006; Robertson et al. 2008; Kelly et al. 2010) and it appears that the seed set of ornithophilous (bird-pollinated) flowers is being reduced by insufficient visitation by birds on the New Zealand mainland. Of the ten ornithophilous-flowered species examined so far, most species had strong pollen limitation with over a third of potential fruits lost due to inadequate pollination service (*Metrosideros excelsa*, Newstrom & Robertson 2005; *R. solandri*, Anderson et al. 2011; *Sophora prostrata*, Kelly et al. 2010; *S. microphylla*, Anderson et al. 2006; *F. perscandens*, Montgomery et al. 2001; *Peraxilla colensoi*, Robertson et al. 1999; *P. tetrapetala*, Kelly et al. 2007; female *F. excorticata*, Robertson et al. 2008; *Alseuosmia macrophylla*, Merrett et al. 2007). Only *Alepis flavida* and hermaphrodite *F. excorticata* did not have substantial pollen-limitation, both are self-compatible, allowing some fruit set in the absence of pollinating birds (Ladley et al. 1997; Robertson et al. 2008). However, selfed seeds may suffer from inbreeding depression (Robertson et al. 2011). This study supports the findings of Robertson et al. (2008), with pollen scores below the level required for adequate fruit set in *F. excorticata* females over much of the mainland, while hermaphrodite *F. excorticata* generally have pollen levels which indicate adequate fruit set.

To determine if reduced seed set caused by inadequate pollination will have population level effects, it is necessary to examine whether the population is seed-limited (Bond 1994). Seed limitation is difficult to measure for long lived plants and has only been examined for three ornithophilous species. Kelly et al. (2007) found *P. tetrapetala*, a stem hemiparasite, to be seed-limited. However, this species is entirely reliant on bird dispersal to attach seeds to host branches and undispersed seeds perish, consequently this species is more likely to be seed-limited than 'normal' plants for which some undispersed seeds can still germinate (Kelly et al. 2007). A study of *R. solandri*, showed that on the New Zealand mainland not only was it severely pollen-limited

but it was also strongly seed-limited, resulting in a reduction in juvenile plants in the population (Anderson et al. 2011). *Fuchsia excorticata* also seems to be seed-limited (Bell 2010). Further studies are required to test whether other pollen-limited ornithophilous plants are also seed-limited.

Additionally, experimental manipulations by Anderson (2003) showed that for three species considered to be entomophilous (insect-pollinated), fruit set was considerably higher when flowers were accessible to both bird and insect pollinators than insects alone. Kelly et al. (2010) considered that bird pollination is important for reproduction in 48 native plant species. Hence it seems that reduced bird densities on the New Zealand mainland are affecting the pollination of many ornithophilous and some non-ornithophilous flowering plants, with demographic consequences for at least some species. However, for some plant species, introduced pollinating species may compensate to some extent (Kelly et al. 2006; Pattemore & Wilcove 2012).

3.4.2 Pollination service and breeding systems

It is important that the status of pollination service is examined in the context of plant breeding systems (Newstrom & Robertson 2005). Only hermaphrodite species without strong inbreeding depression can reproduce independent of pollinators (Newstrom & Robertson 2005). The National Pollination Survey suggests that pollination of hermaphrodite *F. excorticata* plants is generally working well, and low-predator numbers have little effect on boosting hermaphrodite pollination levels. However, it seems likely that pollination and fruit set of hermaphrodite *F. excorticata* stays high at sites with low bird densities through increased self-pollination (Godley 1955; Robertson et al. 2008). Since selfed offspring have very low fitness through strong inbreeding depression (Robertson et al. 2011), hermaphrodite reproduction may still be failing, but is not detected by this current study's measurements of pollen loads.

Pollen loads on female *F. excorticata* plants provide a more reliable indication of current pollination levels and pollinator service. Females are dependent on visits by pollinators as they are not able to self-pollinate, thus pollen loads on female plants are always out-crossed and offspring of female plants have no inbreeding depression (Robertson et al. 2011). Results from this study show that female *F. excorticata* are more vulnerable to mutualism failure than hermaphrodites are, indicated by females having lower amounts of pollen on stigmas at low abundances of birds (Pirongia) or where there is insufficient mammalian predator control (National Pollination Survey). This is consistent with Robertson et al. (2008)'s findings that females are more pollen-limited than hermaphrodites and that females therefore provide a more sensitive visual indicator of pollinator attention.

3.4.3 Competition among birds and pollination

The reduced density and diversity of pollinating birds currently found on the New Zealand mainland may have changed the pollination service received by native plants from what it was in pre-human times. Increasing the density of pollinating birds on the mainland through mammalian pest control may restore pollination to low-reward plants, increase the quality of pollen deposited, and change interspecific interactions.

At reduced bird densities, as currently found over much of the New Zealand mainland, birds may concentrate their foraging on high-reward species and seldom visit low-reward species (Kelly et al. 2010). Observations from island bird sanctuaries, such as Kapiti, Little Barrier and Tiritiri Matangi Islands, where native bird densities are high and probably closer to those found before human arrival, show a wider range of flowering plants are visited by birds compared to on the mainland (Castro & Robertson 1997; Anderson 2003). Castro and Robertson (1997) demonstrated that on Kapiti Island, small flowers usually classified as entomophilous were an important dietary component for tui, bellbirds and hihi, and these flowers were energetically profitable to forage upon. Higher bird densities may force birds to feed on more dispersed or lower-reward food items (Craig & Douglas 1984; 1986). Because female *F. excorticata* flowers produce lower volumes of nectar than hermaphrodite flowers and consequently may be less attractive to pollinators (Delph & Lively 1989), at low bird densities birds may preferentially visit hermaphrodite flowers, exacerbating the effect of females being unable to self-pollinate. However, at high bird densities, competitive interactions may result in greater visitation and pollination of female *F. excorticata* flowers.

Overseas studies have demonstrated links between pollinator movement and outcrossing rates (e.g., Richardson et al. 2000; Hingston & Potts 2005; Karron et al. 2009). Higher bird densities may influence the quality of pollen deposited on stigmas by increasing pollinator movement. Interspecific dominance hierarchies were observed at Maungatautari with tui displacing bellbirds and hihi, and bellbirds displacing hihi, consistent with other studies where the three species coexist (Craig et al. 1981; Craig 1984; Castro & Robertson 1997). At locations where the species co-occur, tui are able to defend flowering trees and have longer feeding intervals during which they may visit most flowers in a particular tree, whereas the subordinate bellbird and hihi are frequently displaced and hence visit few flowers per tree and move between trees more often (Castro & Robertson 1997; Anderson 2003). Birds that only visit a few flowers on each tree before being displaced will accomplish more cross-pollination than those which have long feeding bouts (Ford et al. 1979; Stephenson 1982). Though this effect is smaller than might be first thought if pollen carryover is high (Robertson 1992), as may be the case for bird pollinators (Anderson 1997). If cross-

pollination is increased at sites with higher bird densities, such as at Maungatautari and low-predator sites, then trees at these sites will not only receive greater quantities of pollen but it may also be of greater quality (out-crossed pollen rather than selfed pollen).

Mammalian pest control appears to increase the abundance of native species, while decreasing numbers of exotic and biogeographically recent native species (silvereye, grey warbler *Gerygone igata* and fantail *Rhipidura fuliginosa*) (Innes et al. 2003, 2010). Changed relative abundances will alter competitive interactions and may prevent or reduce access by some bird species to flowers. Although Maungatautari and Pirongia had similar abundances of silvereyes, at Maungatautari fewer silvereyes visited *F. excorticata* flowers of both sexes, and no visits to female flowers were recorded. In contrast, at Pirongia silvereyes were quantitatively important flower visitors. Perhaps at higher densities of tui and bellbirds, as found at Maungatautari, competition reduces visitation by silvereyes. It has been suggested that competition from endemic birds may influence the abundance of silvereyes as indicated by the negative relationship between endemic bird abundance and silvereye abundance at a range of different sites (Diamond & Veitch 1981; Graham & Veitch 2002; Elliott et al. 2010; Innes et al. 2010).

The exclusion of silvereyes by bellbirds and tui may be advantageous to some plants. The small size of silvereyes means that they do not pollinate some large ornithophilous flowers, such as hermaphrodite *F. excorticata* and *S. mircophylla*, and probably *M. excelsa*, and instead function as nectar robbers (Delph & Lively 1985; Anderson 2003; Newstrom & Robertson 2005; Robertson et al. 2008). In comparison, tui and bellbirds are high quality pollinators of most flowers (Delph & Lively 1985; Craig & Stewart 1988; Anderson 1997, 2003; Anderson et al. 2011). Nectar robbers may deter legitimate pollinators by reducing nectar availability (Robertson et al. 2008).

This study, similar to previous studies (Robertson et al. 2008, 2011), assumed that while silvereyes were robbers of hermaphrodite *F. excorticata* flowers they were legitimate pollinators of the smaller female flowers. For pollination to occur it is necessary for pollen to contact the bird in the correct position for deposition on a female stigma. Silvereyes have short beaks, of approximately 14.3 mm (Gill 1980), and are usually unable to access nectar from hermaphrodite *F. excorticata* flowers using the flower opening and instead rob nectar by puncturing the corolla tube (Delph & Lively 1985; Robertson et al. 2008). While hermaphrodite corollas are on average are approximately 20 mm in length (Delph & Lively 1985), lengths vary between 11 and 22 mm (Godley & Berry 1995), and silvereyes occasionally feed legitimately from hermaphrodite flowers with short corollas (J. Iles, pers. obs.). Therefore, although silvereyes can feed from female flowers legitimately, they may have little or no pollen to transfer unless they had also previously legitimately visited a hermaphrodite flower. Further examination of silvereye feeding behaviour is

necessary to determine how frequently visits to female flowers actually result in pollen deposition and therefore whether they are actually important pollinators of *F. excorticata* females.

3.4.4 Restoration of mutualisms

Little attention has been focused on restoring animal-mediated pollination in natural ecosystems (Dixon 2009; Menz et al. 2011; but see Baskett et al. 2011), although ecosystem restoration in general may have unintended (or intended but usually unmeasured) benefits on pollination mutualisms. Given the increase in bird densities with mammalian pest control, we would assume increased bird densities on the mainland would restore bird-plant mutualisms. The only direct attempt to restore a single pollination mutualism between native species (as opposed to an ecosystem-level restoration goal) in New Zealand failed. That attempt was based on the premise that pollination of *P. tetrapetala* was failing due to insufficient numbers of bellbird, their sole bird pollinator at the study site (Kelly et al. 2005). In an effort to increase bellbird numbers, stoats (major predators of many native bird species) were intensively trapped. The stoat trapping dramatically increased bellbird numbers but failed to have an effect on the pollination service received by *P. tetrapetala*. Reasons for the failure are unclear; it may be that while bellbirds increased it was simply not by enough to make a difference to pollination (Kelly et al. 2005).

This study did not examine whether the higher abundance of key pollinating birds at Maungatautari was a consequence of mammalian pest control there. However, the higher abundance of tui and bellbirds, and the presence of hihi, appears to have restored the pollination mutualism to *F. excorticata* at Maungatautari. It should be noted that hihi could not have been successfully introduced to Maungatautari without a very high level of mammalian predator control. Additionally, considering pollination scores across the whole of New Zealand, female *F. excorticata* received better pollination at low-predator sites, presumably because decreased abundance of mammalian pests at those sites allowed pollinating birds to reach higher densities. The National Pollen Survey compared numerous intensively-managed sites to many non-treatment sites, and thus supports the better pollination found at Maungatautari being a result of ecological restoration, rather than some pre-existing, confounding site effect.

Field studies indicate that native bird densities respond positively and often rapidly to mammalian pest control or eradication (O'Donnell et al. 1996; Graham & Veitch 2002; Kelly et al. 2005; Innes et al. 2010). Contrasts between pollination levels on the mainland and offshore islands with high bird density and diversity indicate that pollination is functioning much better on the islands (McNutt 1998; Anderson 2003; Anderson et al. 2006, 2011). Bell (2010) found that seed-limitation in *F. excorticata* on the mainland was related to mammalian pest control, with lower seed-

limitation at sites with pest control compared to sites without pest control, probably because increased bird densities at these sites resulted in improved pollination. Hence it appears that increasing bird density (and diversity) is key to restoring pollination mutualisms.

Fuchsia excorticata suffers from both pollen and seed limitation on the New Zealand mainland, apparently due to decreased pollinating bird densities caused by mammalian predators (Robertson et al. 2008; Bell 2010). This study demonstrates that it may be possible to restore the pollination service to *F. excorticata*. Higher densities of pollinating birds at Maungatautari have improved the pollination service to *F. excorticata*, as indicated by high pollen loads on the stigmas of both female and hermaphrodite plants, and increased pollinator visitation (compared to Pirongia). Analysis of pollen loads on female and hermaphrodite plants from around New Zealand show that hermaphrodites are receiving adequate pollen quantities in most regions (although pollen quality may be inadequate due to inbreeding). However, females at low-predator sites have higher pollen scores than in other regions, indicating that predator control at a site may restore the pollination service to female *F. excorticata*.

Chapter 4

Has Maungatautari Restored Dispersal Services?

4.1 Introduction

Worldwide reductions in the diversity and abundance of bird species has raised concerns over the functioning of ecological services and processes reliant on birds, such as seed dispersal (Cordeiro & Howe 2003; Gaston et al. 2003; Sekercioglu et al. 2004; Terborgh et al. 2008; Wenny et al. 2011). While failure of seed dispersal may increase the risk of plant extinction if plant populations are seed-limited (Bond 1994), documented evidence of dispersal failure causing plant populations to decline is rare (e.g. Christian 2001; Traveset & Riera 2005; Sharam et al. 2009), partly because that link is inherently difficult to prove. However, even if dispersal failure does not cause local extinction, it can still have significant consequences. Seed dispersal by frugivores plays an important role in the colonisation of new habitats and in maintaining the diversity and structure of plant communities (Howe & Smallwood 1982; Robinson & Handel 1993; Harms et al. 2000; Christian 2001; García et al. 2007). Dispersal of seeds by frugivores can enhance germination (Traveset 1998, but see Robertson et al. 2006 and Kelly et al. 2010), and reduce density-dependent mortality of seeds and/or seedlings near the parent (Janzen 1970; Connell 1971; Nathan & Muller-Landau 2000; Packer & Clay 2000; Wotton & Kelly 2011).

In New Zealand, fleshy fruit are found in 59% of tree species (Kelly et al. 2010) and 12 – 14% of the total flora (Lord et al. 2002; Thorsen et al. 2009). Birds are the primary dispersal agents (Clout & Hay 1989; Lee et al. 1991). Following human settlement in New Zealand several bird species which may have been important seed dispersers became extinct: two species of moa with small gizzard stones (*Euryapteryx* spp.), huia (*Heterolocha acutirostris*), piopio (*Turnagra capensis*) and the South Island subspecies of kokako (*Callaeas cinerea cinerea*) (Holdaway 1989; Atkinson & Millener 1991; Lee et al. 1991; Anderson et al. 2006; Miskelly et al. 2008). In addition, compared to pre-human times, several frugivorous bird species are now severely restricted in their distribution. Hihi (*Notiomystis cinta*) were once found throughout the North Island and on Kapiti, Little Barrier and Great Barrier Islands, while saddlebacks (*Philesturnus carunculatus*) were common and widespread throughout North, South and Stewart Islands as well as on many offshore islands (Hooson & Jamieson 2003; Department of Conservation 2005). Both became restricted to only one (hihi and North Island saddlebacks, *Philesturnus carunculatus rufusater*) or a few islands (South Island saddlebacks, *P. c. carunculatus*) (Hooson & Jamieson 2003; Department of

Conservation 2005). At present hihi and saddlebacks are restricted to island bird sanctuaries and a few intensively managed mainland sites where they have recently been reintroduced (Hooson & Jamieson 2003; Department of Conservation 2005). North Island kokako (*Callaeas cinerea wilsoni*) were found throughout North Island, but now only approximately 15 declining or intensively managed fragmented populations remain on the mainland (Innes et al. 1999; Murphy et al. 2006). Additional small populations have been established on island bird sanctuaries (Murphy et al. 2006). Flightless weka (*Gallirallus* spp.) and kiwi (*Apteryx* spp.) are occasional frugivores of fallen fruits (Lee et al. 1991) and have also been reduced in range and abundance (Heather & Robertson 1996).

Currently on the New Zealand mainland the majority of visits to fruit are made by kereru (New Zealand pigeon, *Hemiphaga novaeseelandiae*), bellbirds (korimako, *Anthornis melanura*), tui (*Prosthemadera novaseelandiae*) and silvereyes (*Zosterops lateralis*), although a further 18 species occasionally take fruit (Kelly et al. 2006). Silvereyes are the only species now both widespread and abundant (Robertson et al. 2007). Bellbirds and tui were once widespread throughout the New Zealand mainland but presently have restricted distributions. Bellbirds are absent from most of the North Island, north of about Hamilton, and tui are uncommon in eastern South Island (Robertson et al. 2007). Kereru remain widespread throughout the mainland (Robertson et al. 2007), however they were much more abundant in pre-human times before the clearance of lowland forests and the introduction of mammalian predators (Clout & Hay 1989; Innes et al. 2010). Populations of kereru are gradually declining and although tui and bellbird populations are large and stable they are limited by mammalian predation (Innes et al. 2010).

Predation by introduced mammals is the major cause of decline and limitation in native forest birds on the New Zealand mainland (Innes et al. 2010). There is evidence of predator control increasing abundance of native birds, and additionally, birds are found at higher densities at sites without mammalian predators, such as on offshore islands (see Innes et al. 2010 for a review). In recognition of the effects of mammalian pests on native species, together with improvements in mammalian pest control technologies, intensive large-scale mammalian pest control on the New Zealand mainland is becoming more common, frequently attempting to restore entire communities (Saunders & Norton 2001).

While pollination of some bird-pollinated plants has been shown to be failing and related to reduced densities of pollinating birds on the New Zealand mainland (e.g. McNutt 1998; Robertson et al. 2008; Anderson et al. 2011), the effects of reduced abundance and diversity of dispersing bird species on seed dispersal in New Zealand are less clear. Dispersal of five mistletoe species (*Tupeia antarctica*, *Ileostylus micranthus*, *Alepis flavida*, *Peraxilla tetrapetala* and *Peraxilla colensoi*),

tawa (*Beilschmiedia tawa*) and miro (*Prumnopitys ferruginea*) appears to be functioning well on the mainland (Kelly et al. 2010). Dispersal rates of these species lack a suitable baseline, as they were not compared to areas with high bird densities (and similar to the pre-human situation), so it is difficult to determine an adequate level of dispersal. However, dispersal of *Fuchsia excorticata* and nikau (*Rhopalostylis sapida*) was slower on the mainland compared to an island bird sanctuary where most extant bird dispersers are present (McNutt 1998; Robertson et al. 2008). Dispersal of karo (*Pittosporum crassifolium*) was poorer on the mainland, compared to a nearby island bird sanctuary (Anderson et al. 2006). Dijkgraaf (2002) found suppression of rodents (rats *Rattus* spp. and mice *Mus musculus*) and brushtail possums (*Trichosurus vulpecula*) on the mainland north of Auckland generally increased fruit production of several large-seeded species, decreased the number of fruits damaged by rodents and possums and increased the number of fruit consumed by kereru. Wotton and Kelly (2011) show a potential problem with dispersal failure of taraire (*Beilschmiedia tarairi*) and karaka (*Corynocarpus laevigatus*) causing reduced regeneration, as undispersed seeds suffer from greater seed predation and reduced germination and seedling survival. Although there is no evidence of complete dispersal failure occurring in New Zealand, slower fruit removal rates on the mainland compared to offshore islands where bird densities remain high (and are comparable to the pre-human situation), indicates that reductions in the abundance and diversity of dispersing birds on the mainland may be reducing dispersal rates.

This study aimed to examine whether sites on the mainland with higher densities of dispersing birds receive better dispersal service, compared to sites with lower densities of dispersing birds. In theory a site with virtually all mammalian pests eradicated (Maungatautari) should have higher densities of birds than a site with a lower level of mammalian pest control (Pirongia Mountain) and hence greater dispersal service. Maungatautari is the largest area of mammalian predator-proof fenced forest in New Zealand, covering about 3400 ha, and is free of most mammalian predators. It has most of the extant dispersing birds present, except saddleback and kokako. Kereru, tui, bellbirds and silvereyes were present at Maungatautari prior to fence construction (Innes et al. 2003, 2006). Hihi, whiteheads (*Mohoua albicilla*), western brown kiwi (*Apteryx mantelli*), North Island kaka (*Nestor meridionalis septentrionalis*), takahe (*Porphyrio hochstetteri*, this is the South Island species of takahe, the North Island species *Porphyrio mantelli* is extinct) and yellow-crowned kakariki (*Cyanoramphus auriceps*) had been reintroduced to Maungatautari at the time of this study (C. Smuts-Kennedy, Maungatautari Ecological Island Trust (MEIT), pers. comm.).

The dispersal of fruit from three endemic tree species was examined, *F. excorticata*, tawa and miro. *Fuchsia excorticata* has small fleshy fruit that are consumed by many different species of birds, while tawa and miro have large fruits, and are primarily dispersed by kereru (Robertson et al. 2008; Kelly et al. 2010). There are both quantitative and qualitative aspects to seed dispersal (Schupp

1993; Schupp et al. 2010). This study only examined quantitative aspects of dispersal to provide relative indices of dispersal service (i.e. the amount of time spent visiting fruits or the number of fruits consumed by dispersers, rather than the quality of treatment given to each seed). The assumption was that the greater amounts of visitation and fruits consumed increases the chance of seeds reaching sites favourable for germination and establishment (Schupp et al. 2010).

In this chapter, I (1) establish the relative abundances of key dispersing bird species; (2) determine which bird species are dispersing *F. excorticata* fruits, and examine fruit removal rates of *F. excorticata*; and (3) examine fruiting intensity (fruit crop size) and dispersal quantity of tawa and miro, at both Maungatautari (treatment) and Pirongia Mountain (non-treatment).

4.2 Methods

4.2.1 Study sites and species

The two main study sites, Maungatautari and Pirongia Mountain (referred to hereafter as Pirongia), were the same ones as used in earlier chapters and are described in detail in Chapter 2. Details particular to this study are that although mice were at very low numbers at Maungatautari for most of the study; mouse numbers increased markedly during spring 2011 (from March onwards) due to favourable breeding conditions and a decrease in mouse trapping efforts at the same time (P. Quinn, MEIT, pers. comm.). Mice may eat birds' eggs and nestlings (King 2005); however, they are unlikely to be major nest predators (Badan 1986; Miller & Miller 1995). Mice are seed predators (Williams et al. 2000) and may be seed predators of *F. excorticata* fruits, however they were still at low densities at Maungatautari during *F. excorticata* fruiting. Tawa and miro were fruiting whilst mice were at higher densities at Maungatautari but mice are not known seed predators of either species (Knowles & Beveridge 1982; Ruscoe et al. 2004). Pirongia has many species of mammalian pest present, of these three (feral pigs *Sus scrofa*, possums and ship rats *Rattus rattus*) are important seed predators; however they are not present at Maungatautari. The seed eating larvae of the endemic moth *Cryptaspasma querula* (Lepidoptera: Tortricidae) are present at both sites.

Fuchsia excorticata (Onagraceae) was described in Chapter 3 in relation to pollination. Its fruits are oblong-ellipsoid berries of 5 x 12 mm, which contain approximately 300–600 very small seeds (Burrows 1995; Godley & Berry 1995; Robertson et al. 2008). Fruits ripen from green to purplish-black, and become desiccated and wrinkled when overripe (Robertson et al. 2008). Main dispersers of *F. excorticata* fruit in other areas of New Zealand are bellbirds, tui and kereru (McEwen 1978;

Craig et al. 1981; O'Donnell & Dilks 1994; McNutt 1998; Robertson et al. 2008). Some fruits are also removed by silvereyes, kaka (*Nestor meridionalis*), fantails (*Rhipudura fuliginosa*), yellowheads (*Mohoua ochrocephala*), tomtits (*Petroica macrocephala*), greywarblers (*Gerygone igata*), brown creepers (*Mohoua novaeseelandiae*), and riflemen (*Acanthisitta chloris*) (Burrows 1994a; Burrows 1994b; O'Donnell & Dilks 1994; Williams & Karl 1996). Additionally, fruits are eaten by introduced blackbirds (*Turdus merula*), starlings (*Sturnus vulgaris*) (Burrows 1994b; O'Donnell & Dilks 1994), possums (Burrows 1994c; Dungan et al. 2002) and ship rats (Sweetapple & Nugent 2007).

Tawa (*Beilschmiedia tawa*, Lauraceae), is a tall evergreen tree which grows to over 30 m in height (Knowles & Beveridge 1982). Tawa occurs throughout the North Island in lowland and montane forests up to approximately 850 m a.s.l., and below 450 m a.s.l. in northern South Island as far south as Kaikoura (Knowles & Beveridge 1982). At Maungatautari and Pirongia, tawa is the dominant canopy tree at lower elevations. Tawa has hermaphrodite flowers and produces large ellipsoid-ovoid fruits, which are approximately 14–17 mm wide by 20–40 mm long and contain a single large seed (Poole & Adams 1963; Knowles & Beveridge 1982; Kelly et al. 2010). These fruits are the fourth largest in the New Zealand flora ranked by mean fruit width (Kelly et al. 2010). Fruits ripen in late summer and early autumn changing from green to dark purple (Knowles & Beveridge 1982). Germination occurs after approximately 6 weeks (Burrows 1999), and fruits that have flesh remaining (i.e. have not been through a bird's gut) germinate in the field (Robertson et al. 2006), although at a reduced rate compared to those which have had their flesh removed (Kelly et al. 2010). Fruits are produced annually but fluctuate considerably in abundance (Knowles & Beveridge 1982; Leathwick 1984; Burrows 1999). Tawa fruits are an important food for kereru during summer and early autumn (McEwen 1978; Emeny et al. 2009) and some fruits are also removed by tui and kokako (Booth 1984; Kelly et al. 2010).

Possums, feral pigs and *C. querula* are seed predators of tawa fruits. Possums can destroy large quantities of unripe tawa fruits in the canopy (Knowles & Beveridge 1982; Barraclough 2006 cited by Innes et al. 2010) and may also eat fallen fruit (Knowles & Beveridge 1982; Nugent et al. 2010). Tawa fruit also forms an important seasonal component of feral pig diet (Thomson & Challies 1988). Larvae of *C. querula* are generalist obligate seedeaters and feed on the seeds of both tawa and miro fruits (Sullivan et al. 1995). In the central North Island *C. querula* larvae are a major predator of fallen tawa seed (Knowles & Beveridge 1982).

Miro (*Prumnopitys ferruginea*, Podocarpaceae) is a large tree reaching 25 m, found throughout New Zealand from sea level to approximately 1000 m a.s.l. (Poole & Adams 1963; Salmon 1990). Miro is normally dioecious, although Leathwick (1984) found that most male trees produced a

small amount of fruit on one or more branches. Miro has reddish purple oblong "fruits" that are approximately 12–15 mm wide and up to 20 mm long (Poole & Adams 1963; Clout & Tilley 1992). The endosperm is encased by a woody endocarp, which is then surrounded by a fleshy exocarp; botanically the entire structure is a seed, but it is a fruit functionally and ecologically (Clout & Tilley 1992), and will be referred to as a fruit in this chapter. Miro produces light but regular fruit crops (Beveridge 1973; Leathwick 1984). Fruiting is prolonged and ripe fruits are available during autumn, winter and occasionally into spring (McEwen 1978; Leathwick 1984). Seeds of miro show very slow and protracted germination, taking between 18 months to over four years, but do not need to pass through a bird's gut to germinate (Clout & Tilley 1992). Ripe miro fruits are a significant food source for kereru (McEwen 1978; Clout et al. 1991; O'Donnell & Dilks 1994; Emeny et al. 2009). Bellbirds, blackbirds, tui, and brown kiwi have occasionally been observed consuming miro fruits (Beveridge 1964; Clout & Hay 1989; O'Donnell & Dilks 1994).

Rats are the main exotic seed predator of miro fruits (kiore *Rattus exulans*: Wilmshurst et al. 2008; and ship rats: Beveridge 1964; Daniel 1973; Sweetapple & Nugent 2007). Kiore are no longer present on much of mainland New Zealand (King 2005), but ship rats are ubiquitous in forests throughout the country (King 2005), including Pirongia. Rats cause distinctive damage to miro seeds; the flesh (exocarp) is discarded and the hard endocarp is gnawed through to extract the endosperm, leaving a characteristic hole in the woody endocarp (Beveridge 1964; Wilmshurst et al. 2008). Rats feed on miro seeds in the crown of miro trees and on the ground, and may move seeds to eat at favourable sites (Beveridge 1964; Wilson et al. 2007). This was evident at Pirongia with piles of rodent-gnawed seed on the ground. Miro fruits were not eaten by captive mice in feeding trials, possibly because the seed coat is too hard for them to gnaw through (Ruscoe et al. 2004). Possums normally eat the flesh of miro fruits but not the seeds (Williams et al. 2000; Sweetapple & Nugent 2007). Feral pigs also consume miro fruits (Beveridge 1964; Thomson & Challies 1988).

Kaka are also seed predators of miro fruits and destroy seeds by cracking fruits open to remove the endosperm, discarding the woody endocarp with the flesh still attached (Beveridge 1964). Fruits are often destroyed while unripe (Beveridge 1964). Kaka are present at Maungatautari in low numbers, but are not at Pirongia. Kakariki could possibly damage unripe miro fruits as they destroy totara (*Podocarpus totara*) seeds in a similar manner as described for kaka and miro fruits (Beveridge 1964).

4.2.2 Abundance of key seed dispersing birds

Five-minute bird counts were used as a relative index of dispersing bird abundance at Maungatautari (treatment) and Pirongia (non-treatment). Full details of the five-minute bird count methods are provided in Chapters 2 and 3. In brief, counts were made at 36 bird count stations at Maungatautari and 34 at Pirongia in December 2010. At each visit to a station, a stationary observer recorded all birds heard or seen within a 100 m radius during a five-minute period, following the standardised methodology developed by Dawson and Bull (1975). Each count station was visited twice by one observer who alternated daily between Maungatautari and Pirongia. All stations were counted once before being counting a second time; so any improvements in the observer's ability should be divided between sites.

Important dispersing species examined were tui, kereru, bellbirds, silvereyes and blackbirds. In Chapter 3, the mean counts of all species counted during five-minute bird counts were presented, however only differences in the abundance of three pollinating birds (tui, bellbirds and silvereyes) were analysed. These three species are important dispersers as well as pollinators (Kelly et al. 2006), so the analyses and results will be presented again in this chapter along with those for kereru and blackbirds.

Analysis of five-minute bird counts follows the same methods described in Chapter 3. Briefly, poisson generalised linear models (GLMs) in R (version 2.14.1, R Development Core Team 2011) were used to examine abundances of dispersing bird species at Maungatautari and Pirongia. Each species was analysed separately using the sum of counts at each count station. Site, altitude and altitude-squared, and site by altitude and site by altitude-squared interactions were fitted as predictors. The inclusion of altitude and altitude-squared allowed an estimation of whether altitude effects on bird counts were linear or quadratic. Maximal models were simplified using backward selection based on likelihood ratio tests (the "anova(model1, model2)" command in R). Site was retained in all models as that was the predictor of greatest interest. Fitted means produced by models were divided by two to obtain means per five-minute bird count rather than per 10-minute count.

Maximum counts, a second measure of bird abundance developed by Landcare Research, was used for bellbirds, tui and kereru to examine differences in flock size (Innes et al. 2003, 2006; Fitzgerald et al. 2009). Five-minute bird count stations were separated by 15-minutes walking time rather than distance (mean distance between count stations was 360 ± 12 m). While walking at a steady pace between count stations the maximum number of kereru, tui and bellbirds seen or heard at any one time within 100 m of the observer was recorded. Two consecutive 15-minute walks were then

combined to provide maximum numbers of each species counted during a 30-minute transect. There were 16 sets of 30-minute transects at Maungatautari and 13 at Pirongia, each transect was walked twice whilst doing the five-minute bird counts. To avoid pseudoreplication, the two measurements of each 30-minute transect were summed to provide a single value per transect. Each species was analysed separately using poisson GLMs in R with site as the predictor to examine differences in the maximum number of bellbirds, tui and kereru counted at each site. A quasipoisson distribution was used for tui, as the data were underdispersed (Crawley 2007). Fitted values produced by models were divided by two to provide average values per 30-minute transect.

4.2.3 *Fuchsia excorticata* dispersal

To identify bird visitors to *F. excorticata* fruits, visitation observations were conducted during December 2010 and January 2011. At Maungatautari and Pirongia, six observation stations, that each gave clear views of several fruiting *F. excorticata*, were established. A total of 60 minutes was spent at each station in four 15-minute blocks and each observation station was only visited once per day. During each 15-minute observation period, 8 x 42 binoculars at a distance of 5–10 m were used to record avian visitors to fruit. For each fruit visitor, the bird species and visit duration in seconds was recorded. The number of fruit (both unripe and ripe) present at a station was estimated at each visit, to provide a mean number of fruit present at that station across all observations. As early observations indicated that some birds were eating unripe fruits, the total number of fruit present on a plant, rather than number of ripe fruit, was used to calculate visitation rates. Maungatautari and Pirongia were visited on alternating days to intersperse observation efforts between sites during the fruiting period. For each bird species at a station, visitation rates were calculated as the number of seconds of bird activity per 100 fruit per hour. Fruit visitation rates for each bird species were analysed using non-parametric Wilcoxon rank sum tests in R with observation stations as replicates.

To assess the fruit dispersal service provided by frugivores at Maungatautari and Pirongia, removal rates of *F. excorticata* fruit were examined during the fruit-ripening period, using methods similar to Robertson et al. (2008). In December 2010, roughly 100 fruit (spread over 2–4 branches) were mapped on each of 11 trees per site. The stage of each fruit was noted as *unripe* (green through to red), *ripe* (purple or black – plump and fleshy), or *overripe* (black and shrivelled). These same categories were used on two subsequent visits, separated by approximately a fortnight, to reclassify each fruit. As no flowers were present on the branches at the initial visit, no new fruit appeared during the experiment. To confirm ripe fruit remain on branches in the absence of bird visitors, polyester material was used to bag two branches on two additional trees at each site to prevent bird access. The bagged trees were located away from the experimental trees, in case the bags deterred

bird visitors. Most *Fuchsia excorticata* fruit on the bagged branches remained attached when ripe until becoming overripe, indicating that ripe fruit (and some overripe fruit) remain on branches when not removed by birds.

The rate of dispersal was estimated by calculating the mean proportion of initial fruits present in the ripe or overripe state across visits for each tree (Robertson et al. 2008). It was assumed that good dispersal service by birds would result in more rapid removal of ripe fruit and hence lower abundances of ripe or overripe fruits remaining on the plants, as few fruits would last long enough to become ripe or overripe (Kelly et al. 2004; Robertson et al. 2008). The proportions of ripe and overripe fruits were compared for Maungatautari and Pirongia using a quasibinomial GLM in R. Because the data were over-dispersed, a quasibinomial error distribution and an F test of significance were chosen rather than a binomial error distribution and a chi-squared test (Crawley 2007).

4.2.4 Tawa dispersal

When birds consume tawa and miro fruits the fleshy outer layer is removed by gut passage and a clean, bare seed is defecated (Beveridge 1964; Kelly et al. 2010). Several kereru roosts with excreted tawa and miro fruits underneath were used to determine the appearance of bird cleaned fruit. The total number of tawa and miro fruits per square metre under the canopy of tawa and miro trees was used as an index of fruit crop size (fruiting intensity), and the proportion of fruits collected from the ground underneath canopies that were cleaned by birds was used as an index of dispersal quantity, comparable to Kelly et al. (2010).

During the 2011 fruiting season of tawa, between late January and mid-March, plots of 1 x 1 m were placed under the canopies of mature tawa trees at Maungatautari and Pirongia. All fruits present in the plots were categorised as clean or fleshy, where fleshy fruits had at least some pulp still attached (Kelly et al. 2010). All seed-predated and rotting fruits were collected. Only current season fruit were examined as tawa fruits do not last intact or ungerminated for more than one season (Knowles & Beveridge 1982; Burrows 1999). Trees were located between 300–400 m a.s.l., and diameter at breast height (DBH) was recorded for each tree. Plots were haphazardly allocated to the north, east, south or west side of each tree.

Tawa trees were treated in three ways:

- Group A: One 1 x 1 m plot sampled at date one. A second plot sampled at date two, 180˚ from the first plot (n = 17 trees (10 Pirongia, 7 Maungatautari)).
- Group B: One 1 x 1 m plot sampled at date one, each plot area was marked and all fruits removed after sampling. At date two the same plot was re-sampled (all fruits present were approximately 1 month old), and an additional plot, 180° from the initial plot, was sampled (n = 46 trees (21 Pirongia, 25 Maungatautari)).
- Group C: One 1 x 1 m plot sampled at date two only (n = 20 trees (10 per site)).

This provided a total of 63 plots at date one and 129 plots at date two from 83 individual trees (42 Maungatautari, 41 Pirongia). Approximately one month separated date one and date two. The first plots examined were Group A; these plots were placed with the near edge 1 m from trunks. A preliminary analysis showed these plots had very low proportions of clean fruit; hence it was decided to move subsequent plots to 3 m from trunks (for 16 trees, 3 m was beyond the canopy edge so plots were placed at 2 m). Plots sampled at date two, which had been cleared (i.e. all fruits removed from within the marked area) at date one, were labelled 'cleared'; all other plots were labelled 'not cleared' in the analyses. Cleared plots were used to compare plots where fruit had recently landed (fruit present for less than a month) and plots which had collected fruits for an unknown length of time, to see if they had similar proportions of fruit eaten by birds.

All fruit including unripe (green) fruit were collected. However, unripe fruits were excluded from analyses as it is unclear whether they are consumed by dispersing birds, or, if they are consumed, whether they can germinate. It is unlikely that they are frequently eaten by birds (although a tui appeared to eat green miro fruit at Pirongia). Green fruits may have been aborted by the tree or knocked to the ground by the wind, dispersers or seed predators. All fruits (clean and fleshy, and including seed-predated fruits) were included in the fruiting intensity analysis as a measure of the total fruit crop present at each site. Vertebrate seed-predated fruits were not included in the dispersal quantity analysis as these fruits were probably not available to bird dispersers, as seed predation by possums (of tawa) and ship rats (of miro) often occurs in the canopy (Beveridge 1964; Knowles & Beveridge 1982). *Cryptaspasma*-predated fruits were included in all analyses, as this damage most likely occurred on the ground after fruit had fallen from the tree or had been excreted by dispersers.

Poisson generalised linear mixed models (GLMMs) in the "lme4" package (Bates et al. 2011) in R were used to determine which factors influenced the fruiting intensity of tawa (total number of fruit per square metre). A maximal model was constructed with site, DBH, 'plot treatment' (whether plots were cleared at date one ('cleared') or not ('not cleared')), date (two dates separated by approximately 1 month) and distance (distance of the plot from the trunk), and first order interactions fitted as fixed effects. All fixed effects were categorical variables, except for DBH which was continuous. Individual trees were fitted as random effects to account for repeated measurements from the same trees. A term for DBH was fitted to allow for different tree sizes at Maungatautari and Pirongia, as fruit crop size is often related to plant size (Nathan & Muller-Landau 2000). To find the minimal adequate model, the maximal model was simplified using backward selection based on Akaike information criterion (AIC) values (Crawley 2007). AIC provides a measure of model fit while accounting for the number of parameters included in the model, where the lower the AIC value is, the more parsimonious the model (Crawley 2007). Models were simplified until the deletion of a variable raised the AIC value; the model with the lowest relative AIC value was chosen as the final model (Crawley 2007). This model selection method was used for all GLMMs. The tawa fruiting intensity model was overdispersed, apparently due to the inclusion of both 'not cleared' and 'cleared' plots. 'Cleared' plots had much lower levels of fruit collected in them compared to the 'not cleared' plots. Normally overdispersion would indicate the use of a quasipoisson model, but that option is not implemented for GLMMs. When the analysis was run in a poisson GLMM with just 'not cleared' plots, which made up 76% of the data, the model was not overdispersed. The estimates and significances of variables were similar between both models; hence the model which used the full dataset (both cleared and not cleared plots) is presented.

Binomial GLMMs were used to examine differences in tawa dispersal quantity (proportion of clean fruit out of the total amount of fruit per square metre) between sites. The maximal model had site, plot treatment (cleared/not cleared), date, distance, total fruit (the total amount of fruit (clean and fleshy) per square metre), total fruit squared and all first order interactions fitted as fixed effects. The inclusion of total fruit and total fruit squared allowed examination of whether effects of fruit density on the proportion of fruits bird cleaned were linear or quadratic. Individual trees were included as random effects. Log transformation of total fruit did not improve model fit. Models were simplified in the same manner as for fruiting intensity, and the minimal adequate model is presented.

4.2.5 Miro dispersal

As miro seeds can last in the litter layer for four years or more before germinating (Clout & Tilley 1992), the dispersal service to miro was estimated using the proportion of bird cleaned fruits caught in seed traps placed under the canopies of fruiting female trees. Female trees were identified using 8 x 42 binoculars to check for fruit in the canopy and examination of the leaf litter below each tree for the presence of fallen fruit. Altitude and DBH were recorded for each tree. Seed traps were created using 50 x 65 cm pieces of 1mm mesh polyester material. The bottom 15 cm of each rectangle was rolled over a piece of wood to create a ridge, and this was placed across the slope in the field, to reduce the number of fruits rolling off the trap. Each resulting trap of 50 x 50 cm was secured flat on the ground using pegs at each corner. Four traps were placed under each of 10 trees per site. Traps were positioned midway between the trunk and outer limit of the canopy, at approximately 90° apart where the canopy shaped allowed. Where the canopy was irregularly shaped, traps were placed as evenly as possible to represent the canopy area. Seed traps were set at both sites between 28 March and 1 April 2011, and checked 2, 4, 8, 12 and 16 weeks after placement. At each visit any miro fruits present on traps were removed and classed as fleshy or clean (as for tawa). Damage to fruits was recorded; rats and kaka eat miro fruit leaving characteristic marks (Beveridge 1964). Kaka-damaged fruits collected in seed traps at Maungatautari were all unripe. Rats eat only the endosperm of miro fruits and discard the flesh (Beveridge 1964; Wilson et al. 2007). Therefore, it was not possible to determine if a bird had cleaned the seed eaten prior to it being eaten by a rat or whether a rat had stripped off the flesh before eating the endosperm. Hence, as for tawa, unripe miro fruit were excluded from all analyses and vertebrate seed-predated fruit were included in the fruiting intensity analysis but not in the dispersal quantity analysis.

To remove the nested nature of the data and provide values per square metre, the number of fruits in all four traps at a particular tree at one visit was summed. Poisson GLMMs were used to examine miro fruiting intensity (the total amount of clean and fleshy fruit). A maximal model was fitted with site, DBH, altitude, visit (number of weeks since seed trap placement: 2, 4, 8, 12 and 16 weeks) and first order interactions included as fixed effects. All fixed effects were fitted as continuous variables, except for site which was categorical. Trees were fitted as random effects to allow for repeated measurements taken from the same tree over time. The maximal model was simplified by backward selection based on AIC as outlined above for tawa, and the minimal adequate model is presented.

Binomial GLMMs were used to examine whether dispersal quantity (the proportion of miro fruit cleaned by birds) differed by site, visit (2, 4, 8, 12 and 16 weeks), altitude, DBH, total fruit (the

total amount of fruit per metre squared), total fruit squared and first order interactions. Individual trees were fitted as random effects. The log of 'total fruit' was used as log transformation improved the normality of the model residuals which were previously left-skewed. The minimal adequate model is presented.

4.3 Results

4.3.1 Abundance of key seed dispersing birds

A total of 26 bird species were detected by the five-minute bird counts in December 2010. Mean counts of all species counted are presented in Chapter 2 (Table 2.1). Of the key dispersing species there were significantly higher counts of tui, bellbirds, kereru and blackbirds at Maungatautari compared to Pirongia, while counts of silvereyes were similar at both sites (Figure 4.1, Table 4.1). Altitude tended to have a linear effect on counts, with the exception of kereru (Table 4.1). At both sites counts of tui increased with increasing altitude, while counts of silvereyes decreased with increasing altitude (Tables 4.1 and 4.2). Bellbird counts showed no main effect of altitude but a marginally non-significant site by altitude interaction indicates that counts may have increased more with increasing altitude at Pirongia than at Maungatautari. Similarly blackbird counts showed no main effect of altitude, but a marginally non-significant site by altitude interaction suggests counts at Maungatautari decreased with altitude, while counts at Pirongia increased with altitude. Counts of kereru initially increased with altitude, but the negative altitude-squared term indicates that counts decreased at higher altitudes (Tables 4.1 and 4.2). As previously emphasised in Chapter 3, altitude effects may also be related to time of day effects on bird conspicuousness. It is not possible to distinguish between effects of altitude or time of day (or a combination of both) as counts were always made with increasing altitude throughout the day (although stations were not counted during dawn and dusk when most changes in conspicuousness occur).

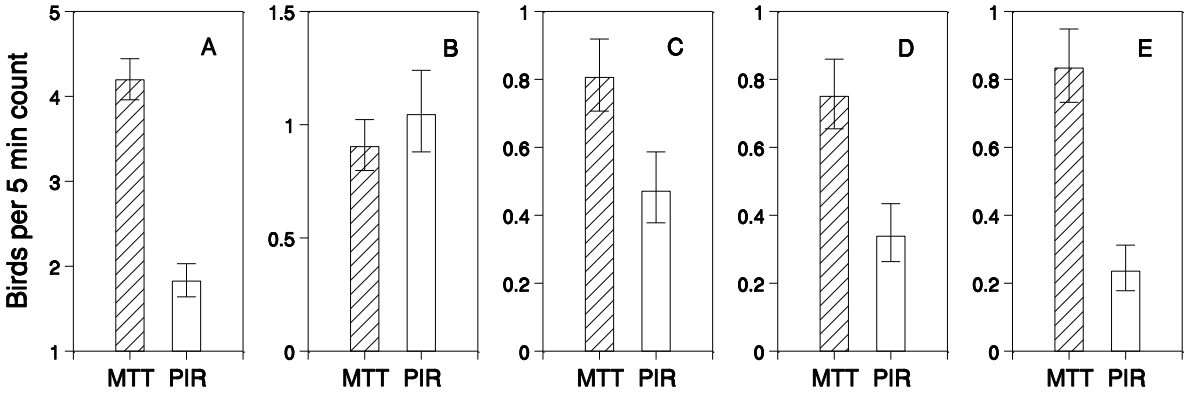

Figure 4.1: Mean number of tui (A), silvereye (B), kereru (C), blackbird (D) and bellbird (E) per five-minute bird count (± SEM) at Maungatautari (MTT) and Pirongia (PIR) in December 2010. Note the different scales of the Y-axes. Values are fitted from poisson GLMs with site as the only predictor.

Table 4.1: Poisson GLMs testing the effects of site, altitude, altitude-squared and first order interactions on the abundance of tui, silvereye, kereru, bellbird and blackbird at Maungatautari and Pirongia. Significant effects are in bold type.

Species	Model	d.f.	Deviance	P(>|Chi|)	% Explained
Tui	Site	1	66.88	**<0.001**	47.05
	Altitude	1	5.23	**0.022**	3.68
	Residual	67	70.023		
Silvereye	Site	1	0.72	0.397	0.49
	Altitude	1	17.72	**<0.001**	15.15
	Residual	67	98.52		
Kereru	Site	1	6.21	**0.013**	4.95
	Altitude	1	24.21	**<0.001**	19.29
	Altitude^2	1	4.60	**0.032**	3.66
	Residual	66	90.48		
Bellbird	Site	1	24.68	**<0.001**	25.16
	Altitude	1	6.59	**0.010**	6.71
	Site:Altitude	1	2.98	0.084	3.04
	Residual	66	63.84		
Blackbird	Site	1	11.13	**<0.001**	14.33
	Altitude	1	0.75	0.386	0.97
	Site:Altitude	1	3.56	0.059	4.58
	Residual	66	62.25		

Table 4.2: Model coefficients from the above poisson GLMs for tui, silvereye, kereru, bellbird and blackbird at Maungatautari and Pirongia.

Species	Model coefficients	Estimate	Std. Error	z value	Pr(>|z|)
Tui	(Intercept)	1.73244	0.18372	9.430	<0.001
	Site(Pirongia)	-0.81828	0.10676	-7.665	<0.001
	Altitude	0.00071	0.00031	2.289	0.022
Silvereye	(Intercept)	1.77560	0.30457	5.830	<0.001
	Site(Pirongia)	0.04737	0.17475	0.271	0.786
	Altitude	-0.00226	0.00055	-4.092	<0.001
Kereru	(Intercept)	-0.23690	1.33200	-0.178	0.859
	Site(Pirongia)	-0.56590	0.23150	-2.445	0.015
	Altitude	0.00724	0.00546	1.328	0.184
	$Altitude^2$	-0.00001	0.00001	-1.988	0.047
Bellbird	(Intercept)	-0.06780	0.54148	-0.125	0.900
	Site(Pirongia)	-2.99280	1.10467	-2.709	0.007
	Altitude	0.00104	0.00093	1.120	0.263
	Site(Pirongia):Altitude	0.00288	0.00170	1.696	0.090
Blackbird	(Intercept)	0.72734	0.54477	1.335	0.182
	Site(Pirongia)	-2.34452	0.88550	-2.648	0.008
	Altitude	-0.00060	0.00099	-0.604	0.546
	Site(Pirongia):Altitude	0.00279	0.00149	1.875	0.061

The second measure of bird abundance, which examined differences in maximum recorded flock size between Maungatautari and Pirongia, showed a greater maximum number of bellbirds, tui and kereru were counted at any one time at Maungatautari compared to Pirongia (Figure 4.2). This difference was significant for bellbirds and tui, but not for kereru (Table 4.3). These results are all consistent with the five-minute bird counts, except that the site difference for kereru was significant for the five-minute bird counts (Tables 4.1 and 4.3). The disparity between five-minute counts and transects is likely caused by the smaller sample size of the transects but may also reflect the difficulty of detecting kereru. Kereru can remain stationary and silent for long periods of time, making them harder to detect while walking compared to standing still.

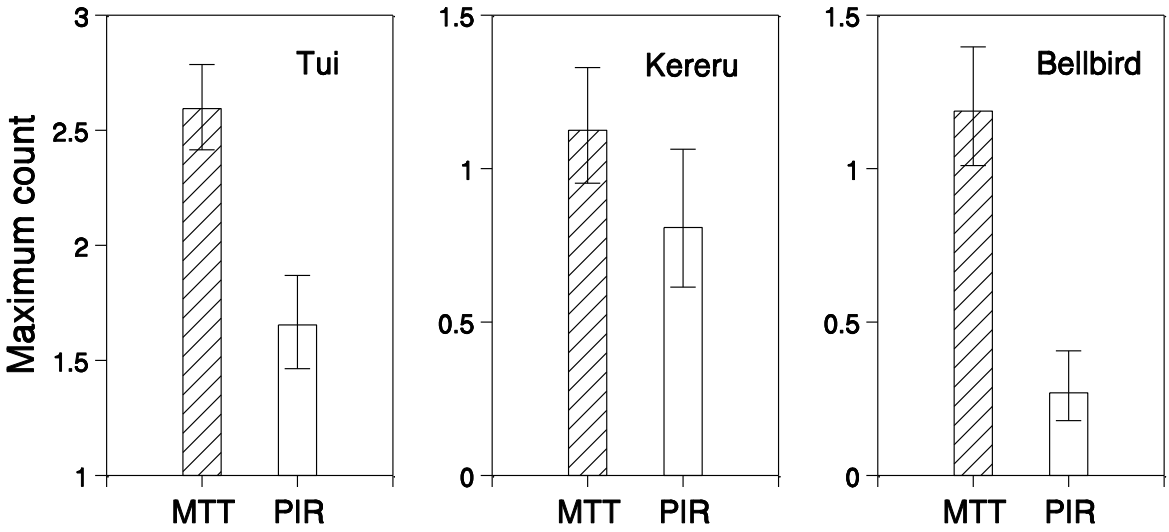

Figure 4.2: The mean maximum number (± SEM) of tui, kereru and bellbird counted at any one time during 30-minute transects at Maungatautari (MTT) and Pirongia (PIR) in December 2010. Values are fitted from GLMs with poisson (kereru and bellbird) and quasipoisson (tui) error distributions and site as the only predictor.

Table 4.3: Generalised linear models testing the effect of site on the maximum number of bellbird, kereru and tui observed at any one time during 30-minute transects at Maungatautari and Pirongia. Bellbirds and kereru were analysed using models with poisson error distributions and tui were analysed using a model with quasipoisson error distribution as data were underdispersed. Significant effects are in bold.

Species	Model	d.f.	Deviance	P(>|Chi|)	% Explained	Error distribution
Bellbird	Site	1	17.53	**<0.001**	45.96	Poisson
	Residual	27	20.61			
Kereru	Site	1	1.49	0.222	4.43	Poisson
	Residual	27	32.20			

Species	Model	d.f.	Deviance	F	P(>F)	% Explained	Error distribution
Tui	Site	1	5.97	**14.096**	**0.001**	33.48	Quasipoisson
	Residual	27	11.86				

4.3.2 *Fuchsia excorticata* dispersal

Bird visitation rates to *F. excorticata* fruit at Maungatautari were significantly higher than at Pirongia, where no bird visitors to fruit were observed during six hours of observation across all stations (Figure 4.3). At Maungatautari, during six hours of observation hihi made nine visits and tui seven visits to fruit. Wilcoxon sum rank tests indicate that differences in visitation between Maungatautari and Pirongia were significant for tui ($W = 3$, $P = 0.010$; $n = 6, 6$ for each test), hihi ($W = 6$, $P = 0.028$) and all birds combined ($W = 0$, $P = 0.003$), but not for bellbirds ($W = 15$, $P = 0.405$), where only one individual was seen visiting fruit (at Maungatautari). While hihi were not detected by the five-minute bird counts, they played an important role in the dispersal service received by *F. excorticata* at Maungatautari. They were the most common visitor to *F. excorticata* fruit and provided 52% of the visitation to fruits at Maungatautari (Figure 4.3). Hihi are not present at Pirongia.

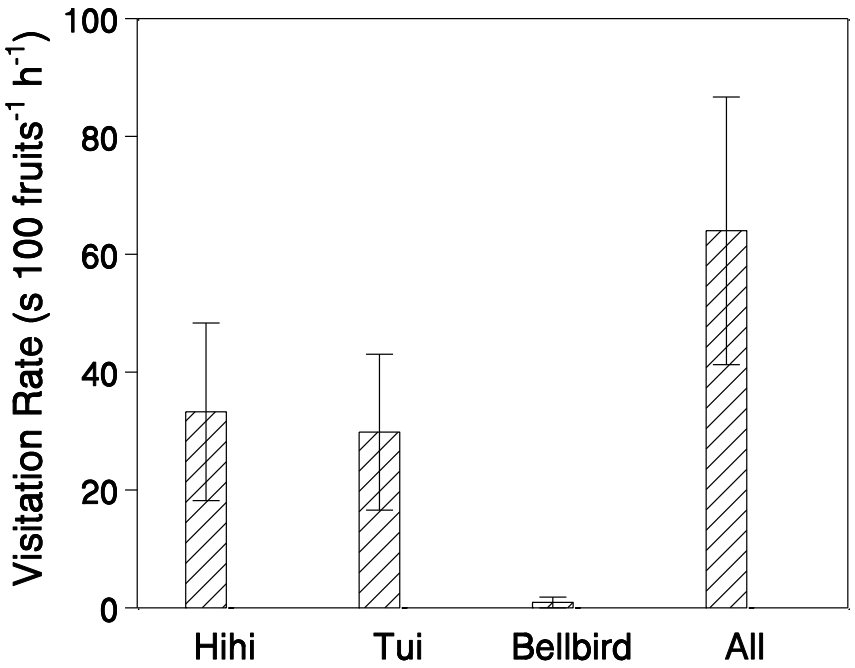

Figure 4.3: Bird visitation rates to *F. excorticata* fruit (mean number of seconds of bird activity per 100 fruit per hour ± SEM) at Maungatautari. Only Maungatautari is shown, as always zero at Pirongia where no visits to *F. excorticata* fruits were recorded.

Fuchsia excorticata fruits were removed faster from branches by birds at Maungatautari than Pirongia, indicated by lower proportions of ripe and overripe fruit remaining on plants at Maungatautari (Figure 4.4). This effect was six-fold and significant (quasibinomial GLM, $F_{1, 20} = 25.981$, $P < 0.001$). There was greater variation in the amount of ripe and overripe fruit remaining on branches at Pirongia (as indicated by the large standard error bars in Figure 4.4) compared to Maungatautari. This indicates that the dispersal service received by individual trees was highly variable at Pirongia, whereas the dispersal service received by trees at Maungatautari was more uniform, with all trees having very low levels of ripe and overripe fruit remaining on branches. While the proportion of ripe and overripe fruits was still quite low at Pirongia (fitted mean of 3.2%), this is an index of dispersal service rather than a measure of absolute dispersal. As *F. excorticata* has prolonged flowering and consequently fruit ripening (Godley & Berry 1995), the absolute number of unripe fruit will always be quite high on plants. Hence at any given time only a small percentage of the initial fruits will be ripe.

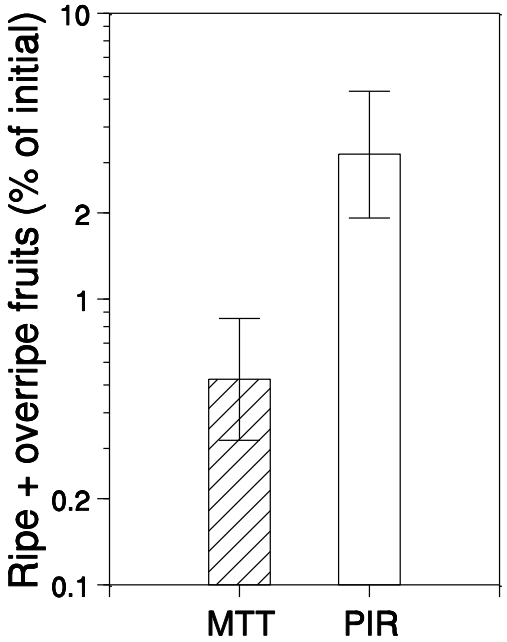

Figure 4.4: The average percentage of ripe and overripe fruit (mean percentage of the initial amount of fruit, ± SEM) remaining on *F. excorticata* branches at Maungatautari (MTT) and Pirongia (PIR) during the fruit-ripening period. Back-transformed fitted means from a quasibinomial GLM. Note log scale on the Y-axis.

4.3.3 Tawa dispersal

In total 10,394 tawa fruits (bird consumed and fleshy) were collected from 192 1m^2 plots under 83 tawa trees. Of these fruits, 197 were unripe and excluded from analysis.

There were roughly twice as many tawa fruits (fleshy and clean) under the canopies of tawa trees at Maungatautari compared to Pirongia (Figure 4.5), and this difference was significant (Table 4.4). Plots contained fewer fruit with increasing DBH at Maungatautari but at Pirongia DBH had little effect on the amount of fruit, as indicated by the site by DBH interaction (Table 4.4). As expected, a greater number of fruits were counted in plots which had not been previously cleared at date one and the site by 'plot treatment' interaction indicates this effect was less strong at Pirongia. More fruits were present in plots at date two, which was later in the fruiting season and larger trees produced more fruit than smaller trees at date two as shown by the interaction between DBH and date. The number of fruit per plot usually increased with distance from the trunk, except for not cleared plots at 3 metres as indicated by an interaction between 'plot treatment' and distance 3 metres. The site by distance interaction was non-significant (Table 4.4), but its removal resulted in a higher AIC so it was retained in the model (model AIC with site:as.factor(distance) included is 1588.0 and without is 1595.3).

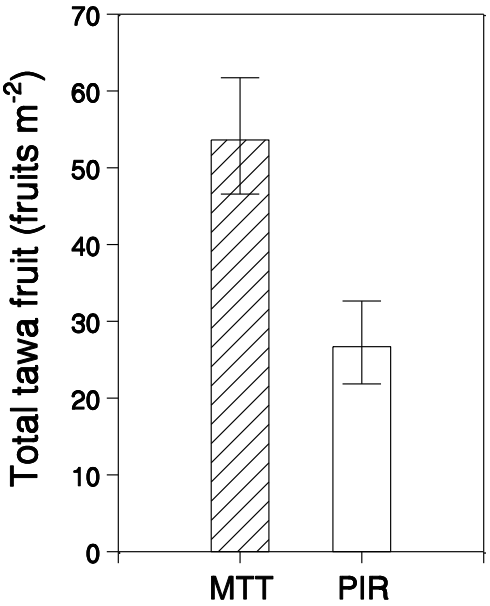

Figure 4.5: The fruiting intensity of tawa at Maungatautari (MTT) and Pirongia (PIR), as indicated by the mean (±SEM) number of all tawa fruit (clean and fleshy) per 1 m^2 plots under tawa tree canopies. Values are fitted from a poisson GLMM with site as the only fixed effect and individual trees as random effects.

Table 4.4: Effects on tawa fruit crop size. Parameter estimates, standard error, z statistics, and P-values of the minimal adequate poisson GLMM testing the effects of site, DBH, plot treatment (whether plots where cleared at date one or not), date (two dates separated by approximately one month), distance from trunk (1, 2 or 3 m) and site x distance, site x code and site x DBH interactions on the total number of tawa fruit (clean and fleshy) collected from $1m^2$ plots under tawa trees. Individual trees were included as random effects. Significant effects are in bold type.

Fixed Effects	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	4.0446	0.4987	8.111	<0.001
Site(Pirongia)	**-2.1086**	**0.7404**	**-2.848**	**0.004**
DBH	**-0.0141**	**0.0046**	**-3.070**	**0.002**
Plot.treatment(Notcleared)	**0.9695**	**0.0731**	**13.267**	**<0.001**
Date(Two)	**0.3408**	**0.0786**	**4.335**	**<0.001**
Distance(2 m)	0.2252	0.3436	0.655	0.512
Distance(3 m)	0.3061	0.3241	0.944	0.345
Site(Pirongia):Distance(2 m)	-0.4856	0.3920	-1.239	0.215
Site(Pirongia):Distance(3 m)	0.0737	0.3598	0.205	0.838
Site(Pirongia): Plot.treatment(Notcleared)	**-0.1667**	**0.0563**	**-2.963**	**0.003**
Site(Pirongia):DBH	**0.0180**	**0.0078**	**2.300**	**0.021**
DBH:Date(Two)	**0.0026**	**0.0009**	**2.833**	**0.005**
Plot.treatment(Notcleared):Distance(2 m)	0.0285	0.1231	0.231	0.817
Plot.treatment(Notcleared):Distance(3 m)	**-0.5335**	**0.0789**	**-6.759**	**<0.001**

The minimal adequate model which best describes the proportion of tawa fruits eaten by birds ("proportion dispersed") is presented in Table 4.5. There was no significant main effect of site on the proportion dispersed. There was a main effect of clearing fruit from plots at the first visit, with a higher proportion dispersed in plots which were cleared of tawa fruit compared to plots which were not cleared. This effect may be because plots which were not cleared included some unripe fruit which by the second date had become brown in colour so were undistinguishable from ripe fleshy fruits, or because cleared plots were only present at the second visit (effect of date). The effect of date was nearly significant, with a higher proportion dispersed at the second date which was later in the fruiting season. There was also a near-significant site x date interaction, indicating that a lower proportion of fruit were dispersed at Pirongia at the second date. A linear relationship with total fruit m^{-2} fitted the data better than a non-linear (quadratic) relationship. The proportion of fruits dispersed decreased with the total amount of fruit present and this decrease occurred more rapidly at Pirongia compared to Maungatautari (Table 4.5); this relationship is illustrated in Figure 4.6, and suggests that the birds at Maungatautari gave better service to large fruit crops than the birds at Pirongia. The decrease in the proportion of fruits dispersed with increasing total fruit was less for plots which were not cleared of fruit. Because there was twice as much (total) fruit at Maungatautari, yet a similar proportion of fruit was bird dispersed, a greater total number of fruit was dispersed at Maungatautari.

Table 4.5: Effects on tawa dispersal quantity. Parameter estimates, standard error, z statistics, and P-values of the minimal adequate binomial GLMM testing the effects of site, plot treatment (cleared/not cleared), date, distance, total fruit and site x date, site x total fruit and plot treatment x total fruit interactions on the proportion of tawa fruit eaten by birds in 1 m^2 plots under tawa trees. Individual trees were included as random effects. Significant effects are in bold type.

Fixed Effects	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	-1.5613	0.2173	-7.184	<0.001
Site(Pirongia)	0.2568	0.2816	0.912	0.362
Plot.treatment(Notcleared)	**-0.8235**	**0.1697**	**-4.852**	**<0.001**
Date(Two)	0.2423	0.1313	1.845	0.065
TotalFruit	**-0.0108**	**0.0017**	**-6.315**	**<0.001**
Site(Pirongia):Date(Two)	-0.3811	0.2102	-1.813	0.070
Site(Pirongia):TotalFruit	**-0.0077**	**0.0032**	**-2.390**	**0.017**
Plot.treatment(Notcleared):TotalFruit	**0.0090**	**0.0018**	**5.015**	**<0.001**

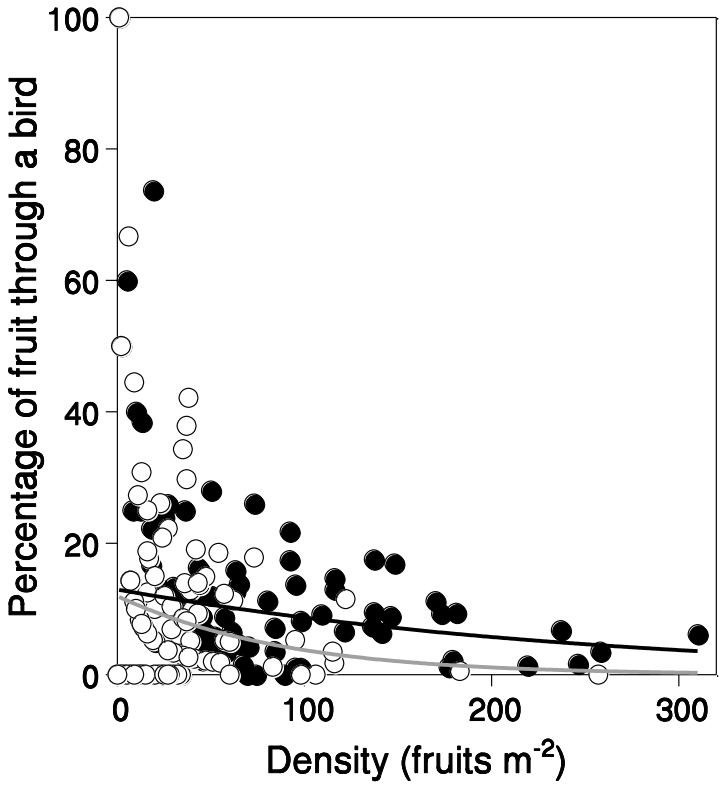

Figure 4.6: Percentage of tawa fruit eaten by birds with increasing fruit density (total number of fruit m^{-2}) at Pirongia (open markers) and Maungatautari (black markers), each data point represents one plot sampled. Lines (Maungatautari black and Pirongia grey) are fitted values from a binomial GLMM with site, total fruit and their interaction as fixed effects and individual trees as random effects. Both dates and cleared and not cleared plots are combined.

4.3.4 Miro dispersal

A total of 570 miro fruits (fleshy and bird consumed) were collected in seed traps under 20 miro trees over four months. Of the 570 fruits, 118 were unripe (green) and excluded from analyses, although 40 (34%) of these unripe fruits came from one miro tree at Maungatautari at the first seed trap check and had been damaged by kaka. A further 117 fruits had been eaten to some extent by vertebrate seed predators (rats or kaka) and were excluded from the analysis of dispersal quantity but not fruiting intensity.

Seed traps under miro trees at Maungatautari and Pirongia caught similar quantities of total miro fruit (clean and fleshy) when all visits were combined (Figure 4.7). The minimal adequate poisson GLMM showed there was no main effect of site on miro fruiting intensity (Table 4.6). The total amount of fruit increased with tree size (DBH) and altitude. The amount of total fruit decreased over time, and a significant interaction between site and visit indicates this decrease occurred more rapidly at Maungatautari than Pirongia. The effect of tree size was less at later visits as shown by a DBH by visit interaction (Table 4.6). The miro fruit crop decreased throughout the period it was measured, indicating that this study continued into the later part of the fruiting season.

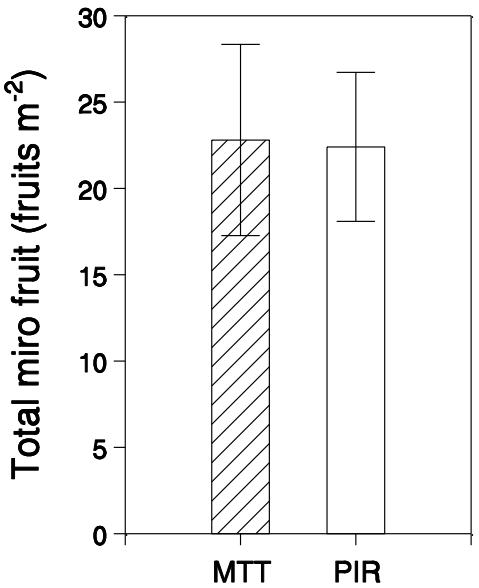

Figure 4.7: The mean total amount of miro fruit (± SEM) caught in 1 m^2 of seed traps under miro trees, all visits combined.

Table 4.6: Effects on miro fruit crop size. Parameter estimates, z statistics and *P*-values of the minimal adequate poisson GLMM testing the effects of site, tree size (DBH), altitude, visit (2, 4, 8, 12 and 16 weeks) and visit x site and visit x DBH interactions, on the amount of miro fruits (clean and fleshy) caught in traps. Individual trees were included as random effects.

Fixed Effects	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-2.0943	0.7936	-2.639	0.008
Site(Pirongia)	0.4721	0.3136	1.505	0.132
DBH	**0.0229**	**0.0043**	**5.351**	**<0.001**
Altitude	**0.0050**	**0.0011**	**4.636**	**<0.001**
Visit	**-0.0868**	**0.0303**	**-2.862**	**0.004**
Site(Pirongia):Visit	**0.0592**	**0.0233**	**2.544**	**0.011**
DBH:Visit	**-0.0012**	**0.0004**	**-3.067**	**0.002**

A significantly greater percentage of miro fruits caught in seed traps were "dispersed" (eaten by birds) at Maungatautari compared to Pirongia (Figure 4.8, Table 4.7). The total amount of fruit had non-linear (quadratic) effects on the proportion of miro fruits which were dispersed (although this was not a significant main effect). The proportion of fruits dispersed was influenced by the interaction between the total amount of fruit squared and visit, with less fruit dispersed later in the fruiting season at higher totals (Table 4.7).

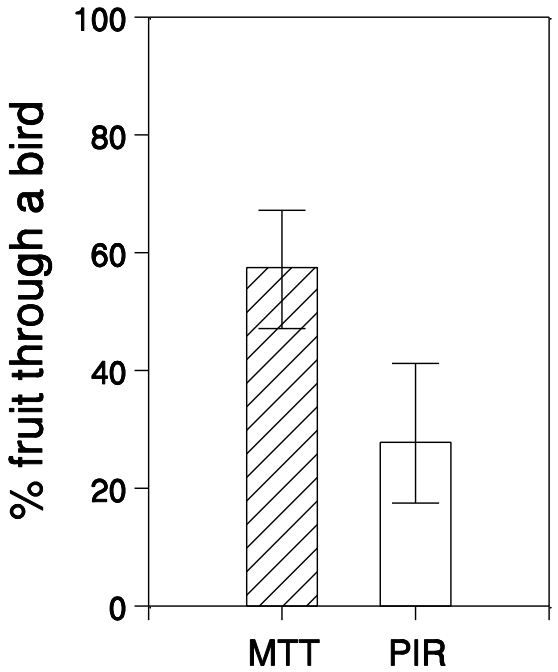

Figure 4.8: The mean (± SEM) percentage of miro fruit dispersed (eaten by birds) at Maungatautari (MTT) and Pirongia (PIR). Values are fitted from a binomial GLMM with site as a fixed effect and individual trees as random effects.

Table 4.7: Effects on miro dispersal quantity. Parameter estimates, z statistics and *P*-values of the minimal adequate binomial GLMM testing the effects of site, visit (2, 4, 8, 12 and16 weeks), total fruit and the visit x total fruit interaction, on the proportion of bird cleaned miro fruits caught in seed traps during the fruiting season. Individual trees were included as random effects. "Total fruit" was log transformed as this improved normality.

Fixed Effects	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.80642	0.62418	1.292	0.1964
Site(Pirongia)	**-1.46991**	**0.61341**	**-2.396**	**0.0166**
Visit	0.04587	0.05858	0.783	0.4337
$\log(\text{TotalFruit} + 1)^2$	0.03871	0.08898	0.435	0.6635
$\text{Visit:}\log(\text{TotalFruit} + 1)^2$	**-0.04902**	**0.02066**	**-2.373**	**0.0176**

4.4 Discussion

The results from this study suggest that all three plant species examined received better dispersal service at Maungatautari than at Pirongia. At Maungatautari key dispersing bird species were more abundant; fruits were removed more quickly from *F. excorticata* plants; and a greater proportion of fruits under tree canopies at Maungatautari had been eaten by birds (for tawa at high fruit densities and for miro at all fruit densities). These positive effects on dispersal service were found across the three tree species in spite of the different fruit sizes and different bird species involved.

There are a number of caveats to be taken into consideration when interpreting the results. These include: the total number of tawa and miro fruits dispersed is likely to be underestimated; there was no control for seed predation; the evaluation of dispersing bird densities was done at a different time from evaluations of dispersal service; and only one fruiting season was examined for each species.

The total proportion of the entire fruit crop of tawa and miro fruits dispersed by birds will be higher than the proportions found by this study, which only applies to seeds collected under the canopy, because while fleshy fruits always fall to the ground near the parent, many seeds eaten by birds are defecated away from the parent and hence are uncounted (Wenny 2000; Kelly et al. 2010; Wotton & Kelly 2011). However, in this study the proportion of bird cleaned seeds is intended only as an index of dispersal rather than an absolute measure of the proportion of the total fruit crop which is dispersed.

There was no control for effects of seed predation on dispersal quantities in this study, as all fruits examined were accessible to seed predators. If *F. excorticata* fruit were removed by rats and

possums at Pirongia we would expect this to decrease the proportion of ripe and overripe fruits present. However there was still a six-fold difference in dispersal between Maungatautari and Pirongia, and ripe fruit should have only been removed by avian dispersers at Maungatautari. Feral pigs, possums and rats may have eaten tawa and miro fruits at Pirongia but not at Maungatautari as they are no longer present there. It is likely that removal by these seed-predators is greater for fleshy fruits rather than clean bird-dispersed fruits (Moles & Drake 1999; Wilson et al. 2007; Wotton & Kelly 2011). Therefore, seed-predation by mammalian pests at Pirongia should cause over-estimation of the bird dispersal service there rather than under-estimation. Nevertheless there was greater dispersal service provided to *F. excorticata*, miro and tawa at Maungatautari than at Pirongia.

Examination of dispersing bird abundance was conducted at a different time from dispersal services. For *F. excorticata*, examination of fruit dispersal in December and January overlapped with the bird counts in December. Bellbirds and tui, visitors to *F. excorticata* fruit, are breeding and relatively sedentary from September until January (Heather & Robertson 1996), so the counts in December should be relevant to measurements of fruit removal in January. It is likely that most kereru, principal dispersers of tawa and miro (McEwen 1978; Clout et al. 1991; O'Donnell & Dilks 1994; Emeny et al. 2009), were still breeding and hence sedentary during the majority of the time when dispersal service to tawa was examined. Kereru lay eggs between September and February (Heather & Robertson 1996) and tawa dispersal service was measured in late January to mid-March.

However, miro dispersal service was examined from late March until mid-July when kereru are no longer breeding (Heather & Robertson 1996). Outside the breeding season at areas where seasonal feeding sites are far apart, kereru may move long distances to good sources of fruit or foliage, whereas in areas with abundant year-round food supply, adult kereru tend to be relatively sedentary (Clout et al. 1991; Mander et al. 1998; Powlesland et al. 2011). It is not known how sedentary kereru at Maungatautari and Pirongia are outside the breeding season, but given the large areas and largely intact native forests it seems that there should be sufficient year-round food supply at the two sites. It is possible that kereru from areas surrounding Maungatautari and Pirongia may move into the forests at certain times of the year. Ideally relative abundances of kereru at Maungatautari and Pirongia should have also been examined during tawa and miro fruiting periods.

Furthermore, fruit crop size and dispersal quantity vary temporally and spatially (West 1986; Nathan & Muller-Landau 2000; Paciak 2002; Kelly et al. 2004; Osada 2005; Bas et al. 2006; Kelly et al. 2010). Thus the results from this study, where only one fruiting season and two sites were examined, should be treated with appropriate caution.

4.4.1 Dispersal service to *Fuchsia excorticata*

Higher numbers of tui, hihi, bellbirds and possibly blackbirds (blackbirds were not seen during visitation observations) at Maungatautari compared to Pirongia were correlated with greater rates of *F. excorticata* fruit visitation and removal at Maungatautari. Low percentages of ripe and overripe fruit were found on *F. excorticata* plants at both Maungatautari (0.52%) and Pirongia (3.21%) compared to those found by Robertson et al. (2008). Mainland New Zealand sites had an average of 15.2% (range ~ 4–25%, taken from their figure 3) of ripe or overripe fruits remaining (Robertson et al. 2008). Kapiti Island, which is a bird sanctuary with high bird densities, had low levels (0.9%) of ripe and overripe fruit (Robertson et al. 2008). The difference between this study and that of Robertson et al. (2008) may be due to slightly different classifications of fruit ripeness. The percentage of ripe and overripe fruits on bagged branches inaccessible to birds in this study (6–15% of all fruit ripe or overripe) was also lower than that on caged branches inaccessible to birds (25–50%) in Robertson et al. (2008).

Fuchsia excorticata fruits at Maungatautari were removed while still unripe, consistent with observations from Kapiti Island (Wilkinson & Wilkinson 1952; McNutt 1998). At high bird densities (such as at Maungatautari and on Kapiti Island) there is greater competition for fruit so if a bird waits for a fruit to become ripe then another bird might eat it first. Conversely, where bird densities are low ripe fruit is present for longer so there is less need to feed on unripe fruits.

4.4.2 Dispersal service to tawa

There was twice the density of total tawa fruit found under the canopies of tawa trees at Maungatautari compared to Pirongia. There are a number of variables which may affect seed production. Environmental factors such as climate appear to synchronise tawa fruit production across large geographic areas (West 1986). Tawa fruit crops may be reduced by colder than average winters, whereas warmer winters produce good fruit crops (West 1986). Another variable could be predation by mammalian seed predators at Pirongia but not at Maungatautari (as only mice remain at Maungatautari). Barraclough (2006 cited by Innes et al. 2010) found that 85–89% of unripe tawa fruits were eaten by possums at Otamatuna mainland island in Te Urewera National Park, and possums may dislodge many otherwise undamaged unripe fruits from the canopy while feeding (Knowles & Beveridge 1982). Possums may also eat ripe tawa fruit (West 1986; Nugent et al. 2010). Tawa fruit crops reaching ground-based traps appear to be greater in areas with possum suppression compared to areas without possum suppression (Dijkgraaf 2002; Nugent et al. 2010). Feral pigs were seen at Pirongia in the areas of the experiments and there was evidence of pig-rooting. Given the importance of fallen tawa and miro fruits in the diet of feral pigs in a similar

forest type (Thomson & Challies 1988), it is likely that pigs at Pirongia consume tawa and miro fruits. As Maungatautari and Pirongia are close to each other (~35 km apart), and study trees were located at similar altitudes (300–400 m), presumably climatic effects on fruit crop size would be similar between sites. Hence, it seems more likely that the difference in fruit crop size between sites is due to greater mammalian predation on unripe and ripe fruits at Pirongia.

Kereru, principal dispersers of tawa and miro fruit (Kelly et al. 2010), were more abundant at Maungatautari than Pirongia in both five-minute and maximum counts, although the difference was significant only for the five-minute counts. Additionally, as previously mentioned, it is not clear how well bird counts in December match abundances when the dispersal service to tawa and miro was examined. Although there was not a main effect of site on the proportion of bird cleaned tawa fruits, twice as much tawa fruit was produced by trees at Maungatautari compared to Pirongia yet the same proportion of fruits were bird eaten. Interestingly there appeared to be differential effects of fruit crop size at Maungatautari and Pirongia on the proportion of tawa fruits eaten by birds. The relationship between fruit crop size and dispersal quantity (the proportion of tawa fruits eaten by birds) was negative at both sites (Figure 4.6), indicating that birds at Maungatautari and Pirongia were satiated by large fruit crops. However, birds at Maungatautari were less satiated by large fruit crops (i.e. coped better with higher densities of fruit) possibly because there were more kereru at Maungatautari.

Proportions of bird-cleaned tawa fruits were relatively low at Maungatautari (13.0%, raw mean, all plots combined) and Pirongia (11.3%) compared with two other studies which examined the proportion of tawa fruits eaten by birds. Roughly one third of tawa fruits caught in seed traps in forest patches near Auckland were bird cleaned (Dijkgraaf 2002). At Blue Duck Scientific Reserve near Kaikoura over nine seasons an average of 50% of tawa fruits were bird cleaned, though this ranged between 12.8 and 79.5% in particular years (Kelly et al. 2010). The 13.0% at Maungatautari is equivalent to the worst of nine seasons at Blue Duck reserve reported in Kelly et al. (2010) (Blue Duck has no mammalian predator control). The relatively low proportion of dispersed tawa fruits found even at Maungatautari may signal relatively poor dispersal service (Kelly et al. 2010), but further data over several seasons would be needed to confirm this.

4.4.3 Dispersal service to miro

Similar amounts of miro fruit were caught at Maungatautari and Pirongia. However, significantly greater proportions of fruit were bird eaten at Maungatautari (59.0%) than at Pirongia (25.8%), indicating greater rates of fruit consumption and hence better dispersal service. There are few previous published reports of miro fruit consumption rates. One kereru at Pelorus Bridge,

Marlborough, consumed an estimated 85% of a single tree's total fruit crop in 1984 (Clout & Hay 1989). Two seed traps under a single fruiting miro tree at Pureora, in central North Island, had 43% and 44% of fruits consumed by birds (recalculated from table 2 in Beveridge (1964) to exclude seed-predated fruits from the total amount of fruit). Unpublished data from seed traps under 10 female miro at Pelorus Bridge over seven years (2004 – 2010) gave an overall average of 50.2% through a bird, with a range from 21.0 to 72.7% in individual years (D. Kelly and J. Ladley, University of Canterbury, pers. comm.). Overall, these comparisons show that the Maungatautari data are reasonably good, while the Pirongia data are among the lowest reported.

4.4.4 Differences in dispersal service of *Fuchsia excorticata*, tawa and miro

A large (six-fold) difference in dispersal service was found for *F. excorticata* between Maungatautari and Pirongia, but differences in dispersal service were less for miro (two-fold) and tawa (only evident at high fruit densities). Differences in dispersal services between tree species may be due to measurement differences, fruit attractiveness, and/or fruit crop sizes.

The dispersal service provided to tawa and miro was measured indirectly using the proportion of bird-cleaned seeds under canopies of tawa and miro trees. It is not known whether the proportion of fruits dispersed away from the parent tree is positively and linearly correlated to the proportion of fruits defecated beneath the parent tree and hence whether it is a good proxy of dispersal service. Although the measurement of *F. excorticata* dispersal service was still indirect, using the proportion of ripe and overripe fruit present on branches, it provides a better indication of the number of fruit not removed from plants by birds. Additionally, given the shorter stature of *F. excorticata* compared to tawa and miro, it was possible to relate rates of *F. excorticata* fruit removal to visitation rates of dispersing birds, allowing confirmation that increased dispersal service at Maungatautari was related to increased disperser activity there.

Fruit attractiveness may also be a factor. Tawa and miro fruits are highly preferred by kereru, forming a large proportion of their diet during summer, autumn and early winter (McEwen 1978; O'Donnell & Dilks 1994; Emeny et al. 2009). Kereru eat large quantities of miro fruits and often little else when miro fruit is available (McEwen 1978; Clout & Hay 1989), frequently defending fruiting trees (Clout & Hay 1989; Clout et al. 1991). Tawa and miro have large sugar-rich fruits and miro fruit is particularly high in protein and zinc (Dijkgraaf 2002). Protein is important for feather growth during moulting and also for the development of eggs and nestlings (Emeny et al. 2009). It may be that because tawa and miro are highly preferred high quality fruits they are the first foods to be foraged upon and can receive good dispersal service even where kereru densities

are quite low. Other, less favoured fruit species may show larger differences in dispersal service between treatment and non-treatment sites at middling kereru densities.

In addition to being a highly preferred fruit, miro has a prolonged fruiting period, as does *F. excorticata*. Twelve years of seedfall data for miro from Pelorus Bridge Scenic Reserve, Malborough, indicates that 50% of the miro fruit crop falls by March (over a period of three months), with 80% fallen by August, and it takes until September (nine months) for all fruits to have fallen (R. Jana, University of Canterbury, pers. comm.). Flowering of individual *F. excorticata* trees occurs over approximately 100 days (Godley & Berry 1995), and fruit ripening occurs over a similar period. Prolonged fruiting may make use of a limited disperser assemblage (Howe 1993), allowing birds to keep up with ripening fruit (i.e. preventing satiation), even when birds are at lower densities (Kelly et al. 2004; Hampe 2008). In contrast, tawa produces large fruit crops which fluctuate in size (Beveridge 1973; West 1986) in a relatively short period (about two to three months, Leathwick 1984; West 1986), perhaps creating a greater risk of satiating dispersers. There is little evidence in the literature of dispersal quantity (proportion of the fruit crop dispersed) increasing with fruit crop size (Christensen & Whitham 1991; Ortiz-Pulido et al. 2007). Instead, dispersal quantity is usually independent of fruit crop size (Davidar & Morton 1986; French et al. 1992; Laska & Stiles 1994; McCarty et al. 2002; Parciak 2002; Kelly et al. 2010) or decreases with greater fruit crop sizes due to satiation of frugivores (Jordano 1987; Murray 1987; Herrera et al. 1994; Herrera 1998; Hampe 2008).

4.4.5 What is a good level of dispersal?

Comparing the dispersal service found by this study with those previously published in the literature is difficult as we do not know what "good" dispersal service is (Kelly et al. 2004; Robertson et al. 2008). Additionally, a range of methods are used to quantify bird dispersal service. Two different methods were used in this study, removal rates (for *F. excorticata*) and the percentage of fruits under the canopy that had been through birds (for tawa and miro). *Fuchsia excorticata* had high rates of fruit removal at both sites, with up to 99.5% of fruits removed from plants at Maungatautari and 96.8% at Pirongia, although these rates will be slightly lower in reality as fruits which naturally fell from plants are included in the dispersed total. A range of fruit removal rates, obtained by following the fate of tagged fruits, are reported in the literature. In a New Zealand study, at least 88% of fruits from two mistletoe species (*P. tetrapetala* and *A. flavida*) were removed by dispersers, indicating good dispersal service (Kelly et al. 2004). In Australia, Willson and O'Dowd (1989) found between 51 and 55% of the fruit crop of the shrub *Rhagodia parabolica* was removed by birds. While French et al. (1992) found an average of 84% of the fruit crop was removed by birds from the shrub *Coprosma quadrifida* in south-eastern Australia. For 22

species in South Carolina, removal rates averaged 72%, although they ranged from 30 to 99% (McCarty et al. 2002). In Mexico, an average of 81% (range 10–100%) of *Casearia corymbosa* fruits were removed (Ortiz-Pulido et al. 2007). These studies indicate that fruit removal rates are highly variable, both within and between species, but we would assume that higher percentages of fruits removed equates to better dispersal service.

The percentage of fruits under tree canopies which have been through birds is less frequently used. In this study low percentages of fruit through bird were found for tawa (raw mean of 12.2% across both sites), while percentages for miro were medium (average of 59.0% at Maungatautari and 25.8% at Pirongia). For the two largest seeded species in New Zealand, percentages of fruit under the canopy through a bird near Auckland have been reported to range between 11 to 53% for karaka and 21 to 36% for taraire (Wotton & Kelly 2011). Again, we would assume that greater percentages of fruit through a bird under the canopy represent greater dispersal service. Given that the removal rates and percentage through bird are different measures of dispersal service it is not possible to compare between them. However, they are suitable for relative measures of dispersal within a species, as used by this study. The two different measures used here indicate that dispersal service received by plants was greater at Maungatautari compared to Pirongia.

4.4.6 Disperser abundance and dispersal service

Previous studies have also found links between reduced disperser abundance and reduced dispersal service, suggesting dispersal service is sensitive to decreases in bird abundance. In New Zealand, contrasts have been made between the mainland and island bird sanctuaries with high abundance and diversity of dispersing bird species. Dispersal of *F. excorticata*, as mentioned previously, was slower on the mainland compared to on Kapiti Island (McNutt 1998; Robertson et al. 2008). On the mainland fewer nikau fruits were dispersed, and over a longer period, than on Kapiti Island (McNutt 1998). Only 20% of karo seeds were dispersed on the mainland near Auckland compared to 94% at an island bird sanctuary (Anderson et al. 2006). In Spain, Herrera et al. (1994) found that birds removed significantly different proportions of the *Phillyrea latifolia* fruit crop at two sites with different abundances of seed dispersing birds. At the site with more seed dispersers 78% of the fruit crop was removed, compared to 33% at the site with fewer dispersers (Herrera et al.1994). Cordeiro and Howe (2003) found a similar effect in Tanzania for *Leptonychia usambarensis*, an endemic tree. Forest fragments, compared to continuous forest, had fewer dispersing birds which made less visits to *L. usambarensis* seeds, removed fewer seeds and reduced the number of seeds dispersed away from the parent tree.

The results from this study are consistent with the idea that Maungatautari is restoring dispersal services to the three native trees examined. Greater abundances of dispersing birds at Maungatautari appear to have resulted in increased bird visitation to *F. excorticata* fruits and higher fruit removal rates there. A larger proportion of the miro fruit crop at Maungatautari was consumed by birds, indicating greater dispersal service. Tawa trees at Maungatautari produced more tawa fruit per square metre compared to Pirongia, and at higher densities of fruit, a greater proportion of tawa fruits at Maungatautari were bird consumed than at Pirongia, indicating that birds at Maungatautari were less satiated by large tawa fruit crops.

Chapter 5

General Discussion

It appears that some bird species and native birds in general have benefitted from the eradication of most pest species from Maungatautari (Chapter 2). Changes in bird abundance at Maungatautari cannot be confidently attributed to the eradication of mammalian pests due to the lack of replication at the site level, and Pirongia receiving some pest control over the same time period making it a poor non-treatment comparison. However, five-minute bird counts and maximum counts in December 2010 indicated large differences in the abundance of tui (*Prosthemadera novaseelandiae*) and bellbirds (*Anthornis melanura*) between Maungatautari and Pirongia (Chapters 3 and 4). The 2010 five-minute counts also showed that there were more kereru (*Hemiphaga novaeseelandiae*) at Maungatautari; although the lack of a significant difference for the maximum counts suggests that this may not be a particularly large effect (Chapter 4).

Higher numbers of tui and bellbirds, and the presence of hihi (*Notiomystis cinta*), at Maungatautari translated into greater bird services provided to *Fuchsia excorticata*, as indicated by increased visitation of flowers and fruit, high pollen loads on the stigmas of both female and hermaphrodite plants, and rapid rates of fruit removal (Chapters 3 and 4). For tawa (*Beilschmiedia tawa*) and miro (*Prumnopitys ferruginea*) the differences in dispersal service were not as large, but it appears that greater numbers of kereru at Maungatautari enhanced dispersal services. For tawa, although there was twice the amount of fruit at Maungatautari compared to Pirongia, a similar proportion of the fruit crop was eaten by kereru, and kereru appeared better able to cope with large fruit crops (Chapter 4). A greater proportion of miro fruits were consumed by birds at Maungatautari compared to Pirongia (Chapter 4). While pest control at Pirongia may be having a positive effect on birds (as indicated by increases in abundance over time, see Chapter 2), bird densities are currently still too low to restore bird-plant mutualisms there (Chapters 3 and 4).

5.1 Do improvements in pollination and seed dispersal matter?

Bond (1994) specified three criteria which influence whether mutualism failure will have demographic consequences for plant populations: the level of mutualist service; reproductive dependence on the mutualism; and the demographic importance of seeds (as outlined in Chapter 1). This thesis only measured the level of mutualist service received, but it is possible to evaluate the other criteria to determine how important restoring mutualism service is for the continued existence

of the selected species' populations (Table 5.1). The restoration of *F. excorticata* pollination and dispersal services observed at Maungatautari (Chapters 3 and 4) is likely to have positive effects on *F. excorticata* populations through increased seed production and dispersal. *Fuchsia excorticata* has a high reproductive dependence on pollination (Table 5.1). The importance of dispersal for *F. excorticata* reproduction requires further investigation; Burrows (1995) found that flesh removal of *F. excorticata* increased germination in petri dishes. However, I am unaware of a study which has examined germination success of cleaned and fleshy *F. excorticata* fruits on soil. The data from Kelly et al. (2010) on a wide range of other native fleshy-fruited species, and the existence of a seed bank, suggest frugivore gut passage is unlikely to be required for germination. Seed dependence of *F. excorticata* is moderate to high as *F. excorticata* is a partially seral species which over time is replaced by other trees (Robertson et al. 2008). Furthermore, *F. excorticata* appears to be seed-limited (Bell 2010), meaning that the production and dispersal of seeds is necessary for its persistence.

While the dispersal services to tawa and miro appear to have been enhanced by increased kereru densities at Maungatautari (Chapter 4), this may have less impact on population persistence (Table 5.1). Avian gut passage is not necessary for germination of tawa or miro seeds (Clout & Tilley 1992; Robertson et al. 2006; Kelly et al. 2010). However, density-dependent effects of reduced dispersal may be important; particularly seed-predation by introduced mammals (Moles & Drake 1999; Wotton & Kelly 2011), but this requires examination. If low densities of birds disperse a smaller proportion of seeds, more undispersed fruit will fall beneath the parent. Survival of seeds and seedlings beneath the parent is low when distance and/or density-dependent processes are occurring (Janzen 1970; Connell 1971; Howe & Smallwood 1982; Packer & Clay 2000; Wotton & Kelly 2011). A recent New Zealand study highlighted the importance of dispersal for two large-seeded New Zealand species. Dispersal of karaka (*Corynocarpus laevigatus*) and taraire (*Beilschmiedia tarairi*) seeds decreased seed predation and increased germination, seedling survival and growth (Wotton & Kelly 2011). Recruitment was very sensitive to reduced dispersal, especially when the percentage of the fruit crop consumed by birds dropped below 30% (Wotton & Kelly 2011). Taraire is congeneric with tawa, hence the low proportions of tawa seeds consumed by birds at Maungatautari and Pirongia might be having significant detrimental effects on tawa recruitment.

Table 5.1: Degree of mutualism restoration at Maungatautari. Examination of the level of mutualist service, mutualism restoration at Maungatautari, and reproductive and seed dependence on each mutualism for the studied mutualisms.

Mutualism	Level of mutualist service	Was the mutualist service restored at Maungatautari (MTT)?	Reproductive dependence on the mutualism	Seed dependence
Fuchsia excorticata pollination	Three effective bird pollinators at MTT (bellbird, tui & hihi) Generalist pollinators – visit many ornithophilous and some entomophilous flowered species (Castro & Robertson 1997) Substitution: possibly silvereyes for females, but evidence suggests not (low female pollen scores at sites where silvereyes are numerous (Robertson et al. 2008, Chapter 3))	Yes, greater abundance and diversity of pollinating endemic bird species has resulted in increased flower visitation, and high pollen loads on both female and hermaphrodite flowers (Chapter 3) [Mutualist service also appears restored at National Pollination Survey (NPS) low-predator sites, as indicated by pollen loads on female plants (Chapter 3)]	High: Gynodioecious breeding system Females: pollen-limited at many sites on the New Zealand mainland (Robertson et al. 2008), but not pollen-limited at sites with abundant pollinators (Robertson et al. 2008; Chapter 3, as inferred from high pollen loads) Hermaphrodites: not pollen-limited (Robertson et al. 2008; NPS data in Chapter 3), BUT inbreeding depression occurs in selfed offspring (Robertson et al. 2011)	Moderate-high: Partially seral species, needs to find next gap (Robertson et al. 2008) Evidence that populations are seed-limited (Bell 2010) But has persistent seed bank (Burrows 1995; Bell 2010)
Fuchsia excorticata dispersal	Numerous dispersers, only hihi, tui & bellbird observed visiting fruit at MTT Generalist frugivores – visit many different plant species Substitution: possibly by introduced blackbirds, not observed visiting fruit at either site	Yes, greater diversity and abundance of dispersing endemic species resulted in greater visitation of fruits at MTT, and very low proportions of ripe and overripe fruit remaining on branches (i.e. rapid fruit removal) (Chapter 4)	Low: Not tested if can germinate in flesh (i.e. if frugivore gut passage is necessary), though the data from Kelly et al. (2010) and existence of seed bank (Burrows 1995; Bell 2010) suggest it is unlikely to be a major problem	Same as for pollination
Tawa dispersal	Predominantly kereru dispersed Kereru are generalist but often concentrate on tawa fruit when available (Emeny et al. 2009) Substitution: possibly some smaller individual fruits dispersed by tui & kokako* (Kelly et al. 2010)	Yes, more kereru at MTT than Pirongia (PIR) Larger fruit crop at MTT but same overall proportion bird eaten as at PIR (so greater total number of fruit dispersed at MTT); birds coped better with large fruit crops at MTT (Chapter 4)	Moderate: Can germinate without gut passage (Robertson et al. 2006) Necessity for recruitment not known. May be high if fleshy fruit, or fruit near the parent, experiences greater seed predation, as for Taraire (*Beilschmiedia tarairi*) (Wotton & Kelly 2011)	Relatively low: Long-lived (200-300 years, Knowles & Beveridge 1982) Can resprout following disturbance (Burrows 1994d) Seeds short-lived but seedlings are long-lived (Knowles & Beveridge 1982)
Miro dispersal	Predominantly kereru dispersed Kereru are generalist but often concentrate on miro when fruiting (McEwen 1978; Emeny et al. 2009) Substitution: some fruits may be eaten by bellbird, blackbird, tui, kokako*, weka* & brown kiwi[#] (Kelly et al. 2010)	Yes, more kereru at MTT than at PIR and a greater proportion of fruits eaten by birds at MTT (Chapter 4)	Moderate: Gut passage not necessary for germination (Clout & Tilley 1992; Kelly et al. 2010). Necessity for recruitment not known, greater seed predation of fleshy than clean seeds (Moles & Drake 1999)	Moderate: Very long-lived (>450 years, Lusk & Ogden 1992) Cannot resprout following disturbance (Burrows 1994d) Has a seed bank (Ogden 1985) Most regeneration occurs away from parent (Lusk & Ogden 1992)

*Not currently at Maungatautari or Pirongia. [#] Western brown kiwi (*Apteryx mantelli*) are in the two smaller enclosures at Maungatautari only.

Both tawa and miro are long-lived (Knowles & Beveridge 1982; Lusk & Ogden 1992) and found in mature forest, potentially buffering them against reduced rates of dispersal and recruitment, although again this needs further examination. Tawa is unusual for a canopy species in that it can resprout following disturbance (Burrows 1994d). Resprouting bypasses the seed stage and provides a mechanism for plants to retain occupancy of a site. Miro does not resprout (Burrows 1994d) increasing its dependence on seed dispersal (Bond 1994), but on the other hand miro is much longer lived than tawa (Knowles & Beveridge 1982; Lusk & Ogden 1992). Seed-limitation is extremely hard to measure for long-lived plants, but miro seeds can survive dormant for at least four years before germinating (Clout & Tilley 1992). Tawa seeds do not last for more than one season without germinating, but seedlings can persist for many years under the canopy in heavy shade (Knowles & Beveridge 1982). So it seems that populations of tawa and miro may be less sensitive to reduced levels of dispersal and thus gain less benefit from increases in dispersal compared to *F. excorticata*.

While improved seed dispersal will not alter plant population size if populations are not seed-limited (Bond 1994), improvements in seed dispersal might increase the frequency of long-distance dispersal events. Seed dispersal allows colonisation of new sites and gene flow between populations (Howe & Smallwood 1982; Shapcott 2000; García et al. 2007). Given the current fragmentation of native forest in New Zealand, the role of long-distance dispersal in colonisation and gene flow is perhaps now of increased importance. Long-distance dispersal events by frugivores occur less frequently than short-distance dispersal events (Howe & Smallwood 1982; Nathan & Muller-Landau 2000; García et al. 2007; Jordano et al. 2007). At increased densities or diversity of dispersers, a greater proportion of the fruit crop may be dispersed, resulting in more long-distance dispersal events and improved chances of seeds reaching new sites or other populations (Cordeiro & Howe 2003; Jordano et al. 2007). This could have important consequences for early seral species, such as *F. excorticata*, which rely on dispersal to colonise recently disturbed sites (Robertson et al. 2008; Bell 2010). Projects, such as Maungatautari, which improve pollination and seed dispersal services to native plants may increase plant population size and/or have positive benefits on gene flow and colonisation.

5.2 Comparison of the restoration of pollination and dispersal services

In New Zealand, where the primary cause of mutualism failure or reduced mutualism service appears to be the reduced density and diversity of bird mutualists, a key component of restoring mutualisms is increasing bird density and in some cases bird diversity. It is possible to compare the processes of pollination and dispersal and hypothesise which factors influence the ease of restoring bird-plant mutualisms.

It might be easier to restore mutualisms which require lower processing rates by bird mutualists, as lower bird densities would be sufficient to provide adequate service. Pollination may be more demanding on bird mutualists than dispersal as there are numerically more flowers than fruits (not all flowers set fruit) and pollination typically requires a more rapid level of service (flowering generally occurs over a shorter time period than dispersal) (Kelly et al. 2004). Thus we might expect that because dispersal is less quantitatively demanding, lower bird densities should be sufficient to provide adequate dispersal service, compared to the densities required to provide adequate pollination. For example, Kelly et al. (2004) found *Peraxilla tetrapetala* at Craigieburn to be pollen-limited but not dispersal limited, although both processes depended upon the same bird species (bellbirds). Within bird pollinated and dispersed species there is likely to be variation in the processing rates required. For instance, the fruiting season of tawa is shorter than that of miro (Beveridge 1973; West 1986; R. Jana, University of Canterbury, pers. comm.). This may explain the difference in dispersal service observed for these species; perhaps the density of kereru at Maungatautari is sufficient to provide adequate dispersal service to miro, but the same density of kereru is less able to provide tawa with good dispersal service.

Mutualisms to plant species with highly attractive fruit or nectar might be easier to restore (or less likely to fail in the first place) compared to less rewarding species, as lower bird densities may be sufficient. Higher bird densities and associated increased competition could be required to increase the level of service provided to plants with lower rewards (smaller volumes of nectar, lower quality fruit or more dispersed flowers/fruit), for example female *F. excorticata* flowers which produce less nectar than hermaphrodite flowers (Chapter 3).

Mutualisms which involve a greater number of bird species may experience more rapid recovery following the implementation of mammalian pest control. In general, dispersal mutualisms may be quicker to restore than pollination mutualisms. Typically more bird species are involved in dispersal, and dispersal systems, overall, are more generalised (Wheelwright & Orians 1982). However, in New Zealand several bird species which are key pollinators are also key dispersers

(Kelly et al. 2006), and both systems are relatively generalised. Thus the number of bird species involved in a particular mutualism (whether it be pollination or dispersal), could be more important. For instance, in the pollination and dispersal of *F. excorticata*, at least three bird species were involved at Maungatautari. Tui and probably bellbirds increased in abundance from mammalian predator control at Maungatautari (Chapter 2: tui increased 2.3-fold between 2002 and 2010 five-minute bird counts; and bellbirds 1.5-fold, fitted rate of increase from Generalised Linear Mixed Models). Changes in hihi (*Notiomystis cinta*) abundance were not quantified but intensive pest control allowed their reintroduction to Maungatautari. In contrast, for tawa and miro, it seems likely that dispersal was primarily dependent only on kereru. Kereru apparently increased at Maungatautari after mammalian pest control (Chapter 2: fitted increase of 2.3-fold between 2002 and 2010). If more species are involved in a mutualism and each species increases, then the cumulative rate of increase and potentially level of service is likely to be higher for mutualisms which involve a greater number of species.

5.3 Mainland islands, fenced sanctuaries and the restoration of bird services

Mainland islands, fenced sanctuaries and other sites with intensive mammalian pest management directly benefit native plant and animal species (Saunders & Norton 2001; Gillies et al. 2003; Innes et al. 2010; Moorcroft et al. 2010; Watts et al. 2011; Innes et al. 2012), and may also indirectly benefit the bird-plant mutualisms of pollination and seed dispersal by increasing bird mutualist density.

It has been suggested that in the conservation and restoration of mutualistic interactions it is important to recognise and then manage or restore species which interact strongly with other species, because of their effects on ecosystem functioning (Memmott et al. 2004; Traveset & Richardson 2006; Kaiser-Bunbury et al. 2010; McConkey et al. 2012). Tui, bellbirds and kereru could be considered strongly interactive species due to the large number of plant species they effectively pollinate and/or disperse (Clout & Hay 1989; Castro & Robertson 1997; Kelly et al. 2010) and their role in providing most bird visits, along with silvereyes (*Zosterops lateralis*), to native flowers and fruits (Kelly et al. 2006; Chapters 3 and 4). Tui, bellbirds and kereru remain over most of the New Zealand mainland (Robertson et al. 2007) and respond positively to mammalian pest control (Chapter 2 and tui, Innes et al. 2004; O'Donnell & Hoare 2012; bellbird, Graham & Veitch 2002; Kelly et al. 2005; O'Donnell & Hoare 2012; kereru, Clout et al. 1995; Innes et al. 2004). Thus the pollination and dispersal benefits observed at Maungatautari from higher bird mutualist densities might extend to other plant species there, and also to other sites

where bird densities are increased through mammalian pest control. Low-predator sites in the National Pollination Survey (NPS) support the idea that *F. excorticata* plants in other areas with intensive mammalian pest control also receive improved pollination service (Chapter 3).

Management at mainland islands and other sites should aim to raise the abundances of these key bird species, because their densities are insufficient over much of the mainland to provide adequate pollination to many ornithophilous species (Kelly et al. 2010; Anderson et al. 2011; *Fuchsia excorticata* at Pirongia and NPS females, Chapter 3) and possibly also dispersal services (McNutt 1998; Anderson et al. 2006, Chapter 4). Soulé et al. (2003) advocate maintaining or restoring species to "ecologically effective densities", where the density and range of a species is sufficient to maintain critical interactions (such as pollination and seed dispersal) and help ensure against ecosystem degradation. In other words, lift the species above the level which Sekercioglu et al. (2004) called "functionally extinct".

The mutualist densities required to be effective will be context specific (Soulé et al. 2003) and the relationship between mutualist density and the level of service they provide might be non-linear (Soulé et al. 2003; McConkey et al. 2012; Figure 5.1). One reason that the relationship may be non-linear is density-dependent foraging behaviour resulting from intra-specific and inter-specific interactions (McConkey & Drake 2006; McConkey et al. 2012). It is possible the relationship between bird density and bird service is non-linear for low reward species or species with dispersed flowers or fruit. When bird mutualist abundance is initially low, increases in bird abundance have little effect on the amount of bird service received by low-reward species as birds concentrate their feeding on high reward species. However, when a critical threshold is reached, competitive interactions between birds results in rapid increases in service provided to low reward plants with increases in bird density (Figure 5.1B). Alternatively, at low densities birds might be able to defend a single flowering or fruiting tree which provides all their energy requirements, resulting in low pollen transfer or seeds being excreted beneath the fruiting tree, again once a critical threshold of bird density is achieved increased competition may mean that birds are no longer able to effectively defend a tree.

Mainland islands, fenced sanctuaries and other areas with pest control might act as important sources of birds and genetic material for surrounding unprotected areas, which usually have lower bird densities. As bird populations increase within controlled areas they may forage in surrounding uncontrolled areas or disperse into them. For example, Landcare Research data indicate that tui abundance in private gardens within 10 km of Maungatautari doubled following the near-eradication of all mammalian pests from Maungatautari (Innes et al. 2012). Movement of birds between controlled and uncontrolled areas may provide greater pollination and dispersal services to

plants in uncontrolled areas and increase gene flow, through the transportation of pollen and seeds, between these areas.

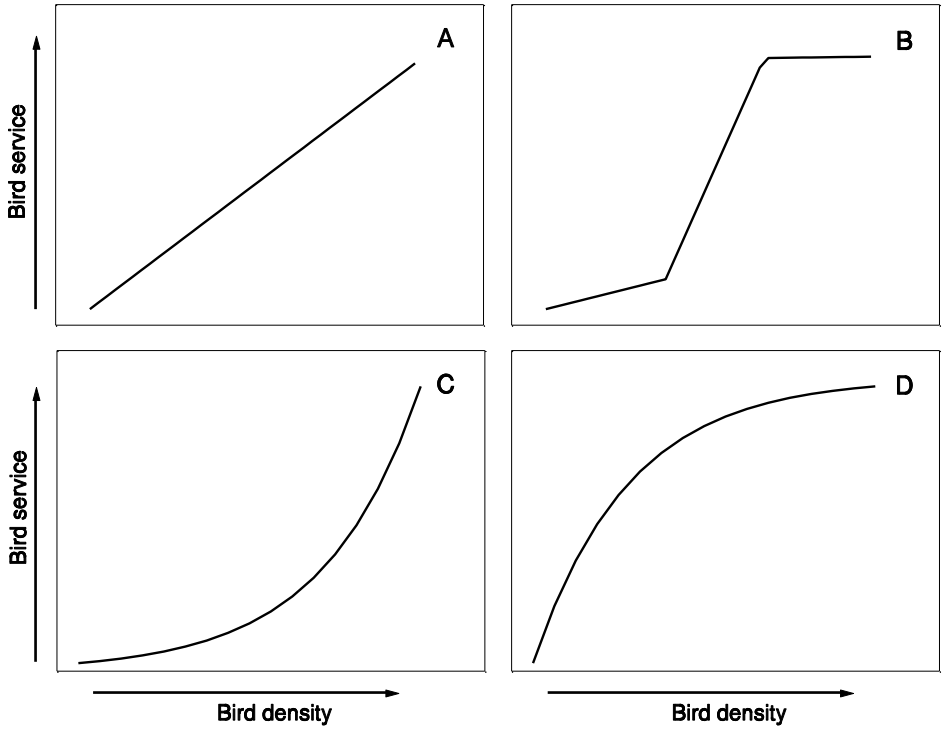

Figure 5.1: Hypothetical relationships between the density of bird mutualists and the resulting level of bird service (pollination or seed dispersal). These relationships may be linear (A) where a given increase in bird density always provides the same increase in bird service, or they may be non-linear (B, C & D). For example, in (B) at low bird densities there is very little increase in service gained with increases in bird density, until bird densities reach a certain threshold and then the service received by plants increase rapidly, until the level of service provided is saturated (i.e. all flowers pollinated or all fruits dispersed, or the maximum density of birds for a given area is reached). Alternatively, increases in bird density may result in accelerating (C) or decelerating (D) gains in bird service.

For plants which are bird pollinated and bird dispersed, such as *Fuchsia* spp., mistletoe species (*Peraxilla* spp. and *Alepis flavida*), and puriri (*Vitex lucens*), restoration of pollination service which increases fruit set may interact with dispersal. Larger fruit displays might mean birds are more attracted to feed upon fruits; namely restoration of pollination service enhances dispersal service (Kelly et al. 2004). Additionally, if greater numbers of fruits are produced this increases the number of seeds reaching sites away from the parent and density-dependent processes (Kelly et al. 2004).

Mainland islands, and particularly fenced sanctuaries, allow the reintroduction of bird mutualists which are functionally extinct on the mainland, such as hihi, saddleback (*Phileturnus carunculatus*) and North Island kokako (*Callaeas cinerea wilsoni*). This study highlighted the importance of hihi as dispersers and pollinators for *Fuchsia excorticata*, providing 52% of fruit and 12% of flower visits to study plants at Maungatautari (Chapters 3 and 4). Hihi have been recorded visiting flowers of many different ornithophilous and entomophilous species on Little Barrier and Kapiti Islands (Gravatt 1970; Castro & Robertson 1997). Hihi visit a wider range of species with entomophilous flower syndromes than tui and bellbirds (Castro & Robertson 1997), so they may be particularly important pollinators of species which are less visited by tui and bellbirds (Anderson et al. 2011). Hihi also visit many fleshy-fruited plant species and, along with bellbirds, tend to visit species with smaller fruit compared to tui (Anderson 1997). Hihi are generally subordinate to tui and bellbirds (Craig et al. 1981; Craig 1985), perhaps forcing hihi to feed from less rewarding species where bellbirds and/or tui are at high densities or when nectar sources are scarce (Armstrong & Ewen 2001). Therefore, it might be necessary to restore a range of bird species and associated interactions to fully restore bird services to native plants.

5.4 The success of Maungatautari

Why has Maungatautari been successful in restoring bird-plant mutualisms, unlike the attempted restoration of the bellbird pollination service to *P. tetrapetala* at Craigieburn by Kelly et al. (2005)? Given that these are two very different systems it is hard to be definite but I raise two possibilities.

(1) Species abundance (quantitative effect). The success of Maungatautari is possibly due to the high level of mammalian pest control there leading to greater increases in the abundance of birds which are broadly present throughout New Zealand. Maungatautari has had essentially all the mammalian predators of New Zealand forest birds eradicated, and only mice remain. This high level of mammalian pest control may be required to create large differences in bird densities and hence bird services. At Craigieburn only stoats (*Mustela erminea*) were controlled (albeit successfully); ship rats (*Rattus rattus*) and possums (*Trichosurus vulpecula*) which are also nest predators of bellbirds remained, although it is thought that rats and possums were at low densities (Kelly et al. 2005). There was a 3.6-fold difference in bellbird numbers between Maungatautari and Pirongia in December 2010 (Chapter 3), whereas at Craigieburn there was a 1.8-fold difference between bellbird numbers at the treatment and non-treatment sites (Kelly et al. 2005).

(2) Species present (qualitative effect). It is also possible that the difference is related to the diversity, or specific identity, of pollinating bird species at each site (Fontaine et al. 2006). Only

bellbirds were present at Craigieburn, whereas tui and hihi, which are also important pollinators, were also present at Maungatautari. As noted above, hihi may be an important mutualist for some plant species, so their absence could mean those plants do not do well, regardless of the densities of bellbirds and tui. Of course, hihi could not be present if ship rat densities were not zero or extremely close to it (Department of Conservation 2005), so this overlaps somewhat with the first point above. Alternatively, there could be another combined quantitative and qualitative effect; perhaps while bellbirds increased at Craigieburn they remained below ecologically effective densities, however the combined abundance of bellbirds, tui and hihi at Maungatautari was sufficient to provide adequate pollination service to *Fuchsia excorticata*.

5.5 Future research

Whether mainland islands, fenced sanctuaries and other sites with intensive mammalian pest control on the mainland, are restoring bird services to native plants merits considerable further attention. The options for future research are numerous, but the following questions could be examined:

- Are pollination services to bird-visited flowers with entomophilous syndromes (e.g., five-finger (*Pseudopanax arboreous*) and tawari (*Ixerba brexioides*)) restored at sites with increased bird densities on the mainland?

- What level of mammalian pest control is required to increase bird density and restore bird services? Are the effects found at Maungatautari (a fenced sanctuary) the same as those found at unfenced mainland islands?

- How important is the restoration of bird diversity in restoring bird-plant mutualisms?

I encourage restoration projects to consider not only individual species' responses to pest control or eradication, such as changes in bird abundance or changes in foliar browse indices, but also to consider changes in ecosystem processes, such as pollination and seed dispersal. Species form complex and dynamic interactions with others (Tylianakis et al. 2008), thus species' responses should not be examined in isolation, but as part of the wider ecosystem. Monitoring of ecosystem processes has been considered too difficult by some (e.g., Brown & Gasson 2008). However, changes in pollination and seed dispersal mutualisms can be measured using relatively quick and simple indices, as shown by this thesis and Anderson (1997), McNutt (1998) and Robertson et al. (2008). The state of mutualisms can provide a valuable measure of conservation and/or restoration success (Kaiser-Bunbury et al. 2010).

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